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CONTENTS

PAGE

Insect Population Problems in Relation to Insect Outbreak ..... *Royal N. Chapman* 261

Population Studies of Soil Insects ..... *Kenneth M. King* 270

Populations of Social Insects ..... *Alfred E. Emerson* 287

Forest Insect Populations ..... *Samuel A. Graham* 301

Insect Populations in Relation to Biological Control ..... *Harry S. Smith* 311

INSECT POPULATION PROBLEMS IN RELATION TO INSECT OUTBREAK[1]

By

ROYAL N. CHAPMAN

The papers of this Symposium on insect populations are related to the environments of soil and forests, to social insects, the biological control of insect populations, and outbreaks of insects. It is intended that the fundamental problems of insect populations should be common to all of the papers. The authors have made an attempt to correlate the subject matter; however, certain duplication in the statement of fundamental principles and examples is important to lend emphasis to the problems that demand the attention of biologists.

The term "outbreak" assigned to the present subject, is defined in Webster's Dictionary as "a sudden or violent manifestation of harmful activity" and concerns itself with the organisms which have increased in numbers or activity. The terms "epidemic," "epizootic," and "epiphytotic" sometimes appearing in literature concern themselves with the temporary prevalence of pests or diseases, implying attention centered upon the host populations designated by the root of the term. Our attention is now centered upon the sudden increase of populations from the standpoint of the populations of the insect pests, whatever they may be. It is realized that there may be cases recorded in literature as outbreaks on the basis of unusual destruction at a time when the population actually was not abnormally high.

In dealing with outbreaks it is inescapable that we must consider the cases in which populations oscillate but remain within what might be termed a steady state or equilibrium, or "the balance of nature" which is so easily expressed in words, phrases and formulae, but so seldom submitted to careful observations or rigid experimentation. The basic problem is concerned with the conditions under which a population departs from the normal oscillations and experiences a sudden increase, the proportions of which may be considered an outbreak. Gause (1934) has stated that in contrast to the "classical oscillations" of the mathematicians in which populations oscillate in a steady state about a mean, there are "relaxation oscillations" arising from a relaxation, or decrease of environmental resistance, followed by a sudden population increase causing "epidemics," or outbreaks. In the latter cases, he says, a certain stage is built up by a continuous process, the conditions become less and less stable, until a stage is reached at which a "discharge" or outbreak must take place.

[1] Published with the approval of the Director as Miscellaneous Paper No. 27 of the Pineapple Experiment Station, University of Hawaii.

In cases represented by insects having a high biotic potential the relaxation of environmental resistance during a single generation, or even for a very short time during a critical part of the reproductive period, may result in a population increase of outbreak proportions. On the other hand, in cases of either a low biotic potential or a slight relaxation in environmental resistance it may be necessary to have several successive periods of reduced resistance occur to make it possible for a population to build itself up to outbreak proportions.

There probably are a number of insects of economic importance which maintain a normal population capable of doing "outbreak damage" in any year if control measures are relaxed, as might be true of the Colorado potato beetle over most of its geographic range. On the other hand, it is probably true of many others, such as most forest insects, that the ordinary fluctuations of the population about its "normal state" are of no particular economic importance; economic destruction coming only under "outbreak conditions."

Turning our attention to the causes of insect outbreaks, we find that certain biologists consider that whenever a change of population level takes place, whether it be within the realm of normal fluctuations or in the category of outbreaks, a change in some physical factor is to be looked for. Bodenheimer (1928), Uvarov (1931), and others consider that these physical factors themselves determine population levels. Nicholson (1933) and others believe that the physical factors merely set the stage which determines the conditions under which the biotic reactions take place. Whether the reactions are accelerated or retarded by physical factors, it is considered that the reactions nevertheless are, of themselves, biotic phenomena.

However, it would seem that, when physical factors become extreme, they pass beyond the realm of conditioning biotic reactions and are of themselves directly responsible for the death of insects and even of entire populations. Regardless of the academic definitions, an extremely cold winter, during which populations of species are greatly reduced in a northern range, would seem to be an example of a physical factor acting directly on an insect population. Conversely, a mild winter may act directly through the lack of the usual low temperature, in permitting unusually large populations, which were present in the preceding fall, to survive and start the succeeding season on a high population level, possibly even one which would be classed as an outbreak. In either of these cases the community of which the populations were a part would experience a biotic reaction the following spring.

It may not be a digression at this point to call attention to the fact that we have a tendency at the present time to develop theories and formulae which seem to satisfy the conditions both of the "steady state" and of "outbreaks" quite apart from detailed observations or critical experimentation centered upon actual conditions and populations. In discussing this problem with a

fellow biologist, he raised the question as to whether we are to have theoretical biologists in the same way that we have theoretical physicists and, if so, whether these theoretical biologists will, like the theoretical physicists, tend to be, as he expressed it, "rather snooty" and look down upon those of us who expose ourselves to the embarrassment of having to harmonize the data from our observations or experimentation with our hypotheses. The history of physics would seem to indicate that both types of research are justified and that each will serve as a check and guide to the other, provided, of course, we maintain a clear distinction between hypotheses on the one hand and facts, on the basis of which we may draw conclusions, on the other hand.

In the field of biology we have had the influence of such mathematicians at Lotka (1925), Volterra (1931), and Bailey (1931), and the theoretical considerations of Nicholson (1933), and others, while Gause (1934) and others have attempted to bridge the gap between the theoretical and the actual by setting up populations to test the hypotheses of the theorists. Theoretical and statistical considerations are important in the formulation of hypotheses to be summitted to rigid proof from experimentation and observations in nature, or both. Data in the raw without reference to theory are often meaningless and may even be misleading. Theories and hypotheses, as such, in the absence of rigid proof, are often confused with principles based upon facts, and when so interpreted, may be misleading in drawing conclusions or in determining courses of action.

In their geographic aspect outbreaks are sometimes purely local, arising either from some purely biotic reaction or from the relaxation of some physical resistance within a geographic area. In other cases the fundamental reactions which create the population may occur in another geographic area from which a migration takes place.

We shall first turn our attention to those outbreaks which occur in local environments. In seeking an understanding of the fluctuations of local populations and the conditions under which they permit populations to assume outbreak proportions, Gause (1934) thinks that the answer cannot be found in the study of populations in nature, because he believes that the entire complex of biotic and physical phenomena is so intricate that there is little hope of a solution. The environmental resistance may be relaxed for some reason thus permitting the biotic potential of the insect, if great enough, to produce a population increase of outbreak proportions. On the other hand there is the possibility, which cannot be overlooked, that some factor may influence reproduction and produce an outbreak.

However this may be, we do have cases in which it has been shown that changes in physical factors, usually departures from the normal condition for the area, have been followed by outbreaks of insects. Leaving aside the academic question as to the direct or indirect action of physical factors, we are at least in a position to know that a variation in a physical factor of the en-

vironment may be followed by an outbreak of an insect. It must be admitted that there is a danger in seeking a solution through a mere statistical correlation between some datum and the outbreak. The existence of a high correlation does not demonstrate cause and effect. The information derived from such a correlation may be helpful in predicting when outbreaks may be expected, but it may contribute little to the understanding of the conditions which produce the outbreak.

The periodicity of the fluctuations of certain animal populations led Elton (1924), Eidmann (1931), Richmond (1938), and others to compare the occurrence of outbreaks of various insects with sun spot cycles. A demonstrated correlation with such a phenomenon might be of aid in forecasting the occurrence of outbreaks. But as to understanding the phenomena involved, it would require a most detailed study to demonstrate that sun spot cycles did affect the abundance of insects directly as a physical factor or indirectly by conditioning a biotic reaction. In some cases the lack of agreement between sun spot numbers and insect populations has led, not to the questioning of a cause and effect relationship, but to the search for an explanation of the lack of correlation in the particular case in hand.

In the case of the pine noctuid, *Panolis flammea,* Eidmann (1934) believes that there is a 10-year periodicity and that in spite of favorable conditions for increase the outbreak collapses, possibly through a biotic reaction, when the population density has exceeded a certain level.

We have many examples of the relaxation of physical resistance which have been followed by insect outbreaks, particularly in connection with temperature and moisture. Examples will be cited with no implication that the cases are the best or most critical on record; they are merely used as concrete illustrations.

Generalizations made purely upon statistical observations from general weather stations may be dangerous. It is entirely possible that the condition in a microenvironment and for a very short period of time may be the critical one. Thus, mean temperatures, isotherms, isohyets and other statistical information may often furnish a valuable suggestion as to possible cause of an insect outbreak. But nothing can take the place of a detailed and critical investigation, preferably combining experimentation and field observation, to determine where the relaxation of the environmental resistance has taken place and has permitted the population to exceed its normal bounds. Uvarov (1931) has suggested the use of a modified bioclimograph indicating not only the physical conditions of the environment but the stage in which the insect happens to be at various times.

Barnes (1934, 1935) presents a careful study of wheat midges, showing that weather conditions may control the infestation of wheat, as for example in 1933, when the spring "was early" and the midges emerged three weeks before the usual time and, although the wheat was also earlier than normal,

the emergence of the midges did not coincide with that of the heads of wheat. With only a few days of adult life in which to oviposit in freshly emerged wheat heads such a lack of synchronism in the development was disastrous to the development of the midge population and caused the year 1933 to pass with a low infestation, whereas the numbers of midges emerging as adults might otherwise have given rise to an outbreak condition.

Cook (1926, 1930), Seamans (1923, 1935, 1938), and others have found that outbreaks of the pale western cutworm (*Agrotis orthogonia* Morr.) are predetermined by the soil moisture conditions during the larval period the previous year. Areas of normally low rainfall and high temperature on the treeless prairies have been found to be most favorable for outbreaks. Under these conditions the larvae live and feed below the surface of the ground where the percentage of survival is high. In case of rains during the feeding period the larvae are forced to the surface of the soil where they are exposed to parasites and predators which Seamans (1935) says are present not only in greater numbers but also in greater variety during wet weather. Hence the number of larvae which are destroyed by parasites and predators is roughly proportional to the number of wet days during the larval period. This is apparently a case of a physical factor conditioning a biotic reaction.

Turning our attention to biotic relaxations which may permit an insect outbreak, there is evidence (Pickles, 1933), that outbreaks of the sugar cane froghopper, normally controlled by the muscardine fungus *Metarrhizium anisopliae,* occur at four- or five-year intervals, and this is apparently due to the fact that there is insufficient moisture for the growth of the fungus in the early part of these years. In the dry season the situation is further complicated by the accumulation of the unhatched eggs of the froghopper which results in wholesale hatching with the onset of the wet season (Urich, F. W. and A. Pickles, 1931). Since, however, biological control of insect populations is the subject of another paper of this Symposium, further examples will not be cited.

Attention will now be turned to the cases in which outbreaks are due to invasions or migrations of insects from other geographic areas. Many of the notable insect outbreaks are traceable to migration, as in the classical case of locusts. The problem is a complicated one involving: (1) a series of conditions which make it possible for a population of outbreak proportions to be produced in one or more geographic areas; (2) conditions which bring about a migration reaction on the part of the insect populations; (3) conditions which make it possible for them to settle upon another area and become established as outbreak populations.

Uvarov in 1933, from his study in Iraq and Syria, has shown that there may be restricted localities or "reservations" in which locusts survive in considerable numbers, even during the years of extreme physical conditions. Here the locusts may thrive and lay eggs in large numbers. When the eggs

hatch, populations build up very quickly and the result of the crowding of the population is a migration to other areas where they appear in outbreak numbers. The special problem of the "migration phase" stressed by Uvarov, on the basis of work in Europe and Asia, Uichanco and Gines (1937), in the Philippines, and others, is viewed by Key (1938), as a biotic reaction to population density resulting in coherent swarms, whatever else may be involved in the genetics and morphology of the case.

After a study of grasshopper outbreaks in Australia, Key (1938) concludes that while there may be some superficial appearance of periodicity, one must go very much deeper if an understanding of the causes of the outbreaks is to be obtained, and a dependable prediction made a basis of rational control. This author believes that the best that can be hoped for is a very broad general correlation between meteorological conditions as recorded and reported and grasshopper outbreaks, because: "(1) While the period over which meteorological factors are of importance in relation to a given outbreak is not known, it is obvious that the precise incidence, both in time and space, of such a factor as rainfall may be of the utmost importance. Three inches of rain spread over a month during which an egg-bed is developing may promote a very high hatch; half an inch during the egg-stage followed by 2½ inches falling in two hours a few days after hatching may spell the end of an outbreak. Similarly, a fall of several inches may be registered at a meteorological station, while an extensive egg-bed 10 miles away may receive no rain. (2) The influence of meteorological factors may be obscured in certain localities by differences in soil or vegetation, or by biotic factors such as the activity of parasites and the application of control measures. (3) The most favorable climatic conditions may fail to produce an outbreak owing to the extremely low ebb to which the population may have been reduced by the previous activity of unfavorable conditions of one kind or another."

Carter (1930), Severin (1933), Piemeisel and Lawson (1937) have shown a similar situation in connection with the sugar beet leafhopper, *Eutettix tenellus*. The insect breeds in the semiarid districts and may reach considerable proportions on the desert where, if conditions are favorable for the continued growth of host plants, it may remain and go into the winter in large populations. If, in the succeeding year, the host plants on the desert dry up, the insect population, which may have reached large numbers, may migrate to settle upon the beet fields. The course of these migrations, over a distance of even 200 miles, has been followed by Dorse and Davis (1937) by a technique of sampling populations from experimental plots placed in the desert and maintained by irrigation. The successive appearance of the populations on these plots between the breeding area and the sugar beet area traces the progress of the migrations of the sugar beet leafhopper from the desert breeding grounds to the irrigated beet fields, where they may occur in outbreak proportions.

The green bug *"Toxoptera graminum"* was found by Wadley (1931) to fall in the category of insects causing outbreaks in northern wheat areas as a consequence of migrations resulting from the synchronism of a series of unusual conditions. Being unable to overwinter in the North the initial population is the result of: (1) Winds of a suitable intensity and duration to carry a population from South to North, which statistics indicate may occur one year in five; and (2) Migrant forms of the insect on the wing at the time the wind is blowing. After the migrants arrive in the northern wheat fields their development to outbreak proportions is dependent upon a dry period such as occurs about one year in four. Wadley concluded that the chance coincidence of the early wind and later dryness might be expected about once in twenty years. His data did not lend themselves to the prediction of the further chance of migrant aphids being present in the South in sufficient numbers for the migration in the years when physical conditions were favorable for migration and subsequent establishment in the North, but such an occurrence seemed well within the realm of probability.

More examples of the migration of insects into areas where they appear in outbreak numbers could be cited, but the object of this paper is to outline problems rather than to summarize the work which has been done on the subject.

Turning our attention to the control of insect outbreaks, we shall consider first the matter of prediction. In the cases where the relaxation of resistance is due to a physical factor, some progress has been made in determining, by careful analysis, in what environment or microenvironment the relaxation of environmental resistance occurs and what stage of the insect it affects. The next step has been to make observations in advance which will predict when and where outbreaks may occur. In the case of the pale western cutworm this has been possible on the basis of rainfall and the conditions which make it possible for eggs to be laid.

Seamans (1938) has geared his predictions to biotic phenomena rather than calendar months and inches of precipitation. "If there are less than ten 'wet' days during the period of larval activity, there will be an increase in the number of cutworms the following year. If there are between ten and fifteen such days during the period of larval activity, there will in all probability be some decrease in the numbers of cutworms the next year. If there are more than fifteen 'wet' days during the period of larval activity, little trouble may be looked for from this insect the following year." (A "wet day" is defined as one during which a cutworm cannot work below the surface of the soil and a farmer cannot use a disk harrow on the surface of the soil.)

If conditions indicate a large population of cutworms the fields which are to be used the following year may be protected by early cultivation and leaving them undisturbed during August and the first half of September for the females will not oviposit in a soil which is covered with a crust.

In the case of migrating insects it is necessary to study the areas from which they migrate to determine whether conditions are such that populations will be built up and that the breeding conditions will encourage the populations to migrate. In the case of the sugar beet leafhopper, *Eutettix tenellus*, the prediction was based upon: first, the minimum temperatures of the winter which were shown to be associated with outbreak conditions the following season; second, on the sampling of populations during the winter to show whether they had survived in potential outbreak numbers under the conditions which had existed. (Carter, 1930; Annand, et al., 1932.)

Prediction of an outbreak sometimes makes it possible for agriculturists to adjust their crops and practices accordingly, and (1) raise a crop which is not susceptible to attack by the insect which is predicted to be abundant; (2) concentrate control measures on breeding grounds before outbreak populations are built up; and (3) be prepared to apply preventive measures to crops before great economic damage is done. Uvarov (1933) says that it will be possible to control outbreaks of locusts by doing preventive rather than remedial work. He says that the locating of the so-called breeding reservations and carrying out control work on them before the populations have reached the point of migration would cost a small fraction of the remedial measures after the locusts have dispersed to agricultural areas.

This brief consideration of some of the problems of insect outbreaks seems to indicate that the most important problem is to get critical research done: (1) on the fundamental problems of populations and the causes of their fluctuations, and (2) on the ecology of "outbreak pests" in advance of the outbreaks. This means working on a species of insect at times when it is not thought of as of any economic importance, even though there may be demands for remedial work on another species. The same economic demands which have built up great programs in economic entomology have often prevented or interrupted programs of sustained fundamental research which, in the long run, would give the greatest economic return.

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POPULATION STUDIES OF SOIL INSECTS

By

KENNETH M. KING*

Dominion Entomological Laboratory
Saskatoon, Saskatchewan

Soil insects may be defined as including "any insect which at one time or another, in the course of its development from the egg to the fully mature adult, spends some stage or stages of its life-history either on the surface of, or buried in the soil" (Cameron, 1913). In this broad sense the group includes nearly all insects of grassland, ruderal and other communities where the vegetation is comparatively short; but in forests a considerable proportion of the total insect population has no direct relation to the soil or litter. Viewed in this way, the other comparable but overlapping groups are aquatic insects, and those which spend their life upon or in animals or vegetation and in the air. Ecologically, the soil insect group does not constitute a single natural entity, but cuts across and forms a part of nearly all communities.

Even at the risk of being too diffuse, it has appeared best to attempt a balanced summary of the problems in this whole important field. In doing so, it seems allowable to express, even though tentatively, some personal opinions,[1] with a view to stimulating thought and discussion.

The Soil Habitat and Its Insects

It may be illuminating to list the most striking characteristics of the soil in relation to its insect populations: It is relatively stable chemically, structurally, and in fact in most respects. Variability of physical factors is greatly reduced as compared with conditions above its surface. Its relatively low penetrability hampers insect movements, but nevertheless tends to afford them differential protection from enemies of all kinds, by greatly decreasing the latter's ability to make contact with their hosts. A very sharp gradient of temperature and correlated conditions commonly exists, especially near the surface. As there is little air movement the atmosphere remains saturated or nearly so until the soil moisture content, at a given level, drops below a rather low critical point; but lack of aeration does not seem to be a seriously adverse factor except in places subject to prolonged flooding.

Thus the soil affords refuge from both high and low extremes of temperature;[2] and from wind, evaporation, light and dryness. For insects that

* The collaboration in this research at the Saskatoon Laboratory has become so close that the source even of ideas is often uncertain. The writer therefore desires particularly to acknowledge his indebtedness to his colleagues, especially Robert Glen, A. P. Arnason and L. C. Paul.

[1] Many of the ideas expressed are the outgrowth of periodic studies, maintained since 1923, of the invertebrate populations of both native and ruderal communities, and quantitative work with several crop pests (King and colleagues, '26, '27, '28, '29, '33, '36).

[2] It has been shown (Chapman, et al., '26) that many of the sand-dune insects escape lethal surface temperatures, such as occur daily during midsummer, only by burrowing short distances into the

can burrow in it even slightly, it permits large and relatively easy adjustments to unfavorable conditions, either daily alterations or seasonal changes. On the other hand, the slowness of movement within the soil renders flexibility of food habits of great significance for species or stages confined there. Thus, facultative saprophytes have an advantage (Ghilarov, 1937) in soil over strictly phytophagous forms, species of broadly predacious habits over specific parasites, and general feeders over any others. In this, as in other respects, the abundance of a species may be limited by the requirements of a single restricted stage, especially the young larvae.

Relative to insects, then, the most important soil factors are moisture, temperature and food; while soil texture markedly conditions all factors as well as insect responses. There are often complex interactions. For example, Lane and Jones (1936) found that the effect of submergence on certain wireworms was definitely greater in flooded soil than in pure water, and in both was greatly influenced by temperature.

This brief analysis indicates that soil insects as a group are characterized, relatively, by low mobility, low resistance to extremes of physical factors, and low susceptibility to natural enemies particularly specific parasites and disease; and by a high proportion of facultative saprophytes or predators, and general feeders. Such characterization applies to the species and stages for which existence in the soil is obligatory, especially those which inhabit the deeper layers or spend their entire life in the soil. The contrast is rather sharp between the soil and aerial fractions of the same community. Soil insects, especially those in habitats that are relatively undisturbed, tend to be concentrated near the surface.

Even within a single ecological community, however, the soil insect population is far from being either uniform or constant. The quantity, quality and distribution vary widely both in space and time. Rapid changes occur, some irregularly, others more or less regularly such as daily, seasonal and developmental changes. Lateral and vertical variations occur in response to differences in either the occurrence or growth of food, or in other environmental factors, all allied to "soil heterogeneity." In addition to such variations, and those due to aggregation or social habit, there are many which are more or less accidental as where the numerous progeny of individual parents form temporary concentrations the intensity and duration of which depend upon the mobility of both females and young. This whole question of insect distribution is basic to the development and use of valid quantitative methods.

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soil. On the other hand, at Saskatoon, many years' soil thermograph records, at a depth of three inches under sod, show only a single instance of temperature below zero Fahrenheit (this was — 2.5°F.), and few below + 10 degrees Fahrenheit, although on occasion air temperatures may not rise above — 20 degrees Fahrenheit for a period of several weeks; the buffer action of even the thin layer of snow normally found at Saskatoon is of course very important (Mail, '30) in this connection.

METHODS OF STUDY

Because the development of sound methods of study is fundamental to further progress, the discussion of methods, including the advances already made, is of primary importance. Intensive development in this field is very recent and, although there has been excellent work on different aspects, apparently no general appraisal of principles has previously been made. Consequently it will here be attempted, however imperfectly, to define in general terms what constitutes adequate sampling under various circumstances.

A population study has several more or less distinct phases. These always include size, number, and distribution of the samples; securing and examining them; and recording, tabulating and analyzing the data. Often there are supplementary methods, in which the populations of typically soil insects can be measured by means of symptoms visible at the surface or counts of their stages active above ground. The final important phase of experimentation, required to round out and complete quantitative field observation, is only touched upon in the present discussion.

Rigid standardization of methods in any of these phases is seldom possible or desirable, in view of the great diversity both of conditions and purposes of investigation. Indeed, adaptability to needs and flexibility in response to findings are constantly necessary. No single size, or frequency, or distribution, or intensity of examination, will invariably serve all purposes even within the same project. Nevertheless, certain common objectives and basic principles may be recognized, leading to that increasing comparability of results which is the true aim of standardization. For purposes of comparison, all population data should be expressed in terms of area, i.e., rates of population, or means of conversion shown. Then, too, it is often possible to standardize at least part of the work desired for closest comparison within a project.

Because population studies are very time-consuming, careful planning is especially essential. It must take into account, at every stage, the purpose of the study, the efficient use of time, and the requirements of adequate statistical analysis. The initial plan should provide for the expansion that is always needed as the work progresses, to follow up the leads secured as well as to meet unforeseen developments. Of course, if it is not possible to do sufficient work to give results that are significant in at least some valid sense, it would be better to drop a project altogether. On the other hand, it is not sound to exaggerate the statistical aspect out of all proportion to other phases of the study; nor will biometrical manipulation, however intricate, ever provide a suitable substitute for sound biological judgment. It is always essential, however, to ascertain and clearly show the degree of accuracy maintained in each investigation, and to express the population data in appropriate terms.[3]

[3] It would obviously be futile or misleading to show an estimated population rate of, say, 3,651,520 insects per acre, on the basis of a census of, say, four square-foot samples (though figures such as this frequently appear in print). Even with complete accuracy the multiple would be 10,000 while the actual dependability would be much less. In such an instance, the estimate would be more correctly expressed as 3,600,000, any greater precision being quite meaningless.

For greatest efficiency, the aim should be (1) only for that degree of accuracy which is reasonable in relation to the purpose of the project and the proportion of time that would be required to attain materially greater accuracy and significance; and (2) for a close balance both between the several phases of the project, and, within each phase, between intensity of work and representativeness of coverage. The decisions as to what is "reasonable" and what is "balance" of course call for sound judgment. But in general an excellent procedure is to provide and maintain a basis for judgment by more intensive work in a limited portion of each phase, supplemented by less and less intensive coverage over as much as possible of the remainder.

Size of sample. The area of the individual sample-unit is interrelated with their number and aggregate area. All three must be adapted to population density and distribution, as well as to the general considerations that have been listed. The unit size should be such that the frequencies of both zeros and high counts will be minimized for each common form. An area of about one square foot[4] is ideal for many population studies of invertebrates. A "smaller" area should not be accepted unless it reduces the time per sample-unit sufficiently to permit a corresponding increase of the number of units without material reduction in their aggregate area. "Small" sample-units are definitely worthwhile only where there is a very dense population. This need may often be met by intensive examination of a portion of each unit for abundant forms such as Collembola. On the other hand if there are aggregations, scouting may have to be done to determine their number and frequency, and the average size and density then worked out.

Specifically, if it is found in a given project that, for example, only 40 one-eighth-square-foot samples can be fully handled in the time required for 30 square-foot samples, obviously the latter are preferable because they represent six times the area and population with a reduction in number of only one-fourth. On the other hand, were it possible in a given time to take four times as many one-fourth-square-foot samples as those of square-foot size, such a procedure would, at least in most instances, offer a definitely greater advantage, by giving much greater frequency and the same total area. But this is rarely possible, because there must be taken into consideration the time required, not only for actual examination of the sample but for the whole project. There must be a very large saving of time in any single phase to have much effect on this total. Then, too, "small" sample-units may require even more time in the field than those of convenient working size; for one thing, the requisite precision as to dimensions increases by inverse proportion to area, if the same relative accuracy of data is to be maintained. Exactly where the point of best balance falls, between the two extremes cited, is problematical; but it is suggested that, for example, if the sample size is cut to

[4] More specifically, an area of 1.089 square feet (e.g., 12 x 13.07 inches, or a circle of 14.13 inches diameter), representing 1/40,000th of an acre or approximately 1/100,000th of an hectare, is favored because of the ease of conversion to a basis for easier comparison with data from other studies.

one-fourth, the number must be at least doubled to compensate for the lesser aggregate area included.

Distribution of sample-units.[5] The mode of distribution of the samples is very important. It is our conviction: that even at the beginning of an investigation there should be purposeful selection of sample-unit placement to as full an extent as there is sound basis afforded by prior knowledge, accurate observation and good judgment; that as an investigation develops the mode of sample-unit distribution should be progressively modified in accordance with the new knowledge and experience; and that randomization within the selected subdivisions can usually be accomplished most advantageously by systematic placement rather than by "chance."

In the absence either of dependable knowledge of the mode of distribution of the insects to be studied or of recognizable factors known to affect insect distribution, an investigation must of course begin with methods that are generalized in every respect, including strictly randomized methods of sample placement. Such methods should usually continue also to form a part of it throughout its duration, as a check against possible error.

In most insect population studies, however, there is need and opportunity from the first to make sound selection of sample placement. This will be in relation to visible local variations which, from general knowledge of insects and communities, may be expected to have possible correlations with insect concentration or scarcity. In the early stages, such selection may be in the nature of "scouting," designed the more quickly to reveal local conditions of chief significance. Such procedure will facilitate the further development of special sampling methods. Eventually, with extensive knowledge of the mode of distribution of the species concerned and experience in recognizing points of significance, the main work of a project may become highly specialized, including purposeful selection of the time and place for nearly all sample-units. Even in general population studies there is often great advantage in such purposeful selection of local types, each to be represented by sample-units in number proportional to area. To secure valid averages, the placement of sample-units must then be randomized within each of these apparently homogeneous type-situations.

The force of this can best be realized by considering one or two instances of the more extreme types of insect distribution. The "roadside" grasshopper (*Camnula pellucida* Scudder) lays its eggs mainly within concentrated "egg-beds," which are found chiefly in short grass of certain kinds while type of soil may also have an influence. Even when this species is abundant enough to have a material effect upon an entire community, these egg-beds occur on only a very small proportion of the total area, and are very irregularly placed. It would require an immense amount of strictly randomized soil sampling of an entire community to give any accurate measure of the egg population of this species. But by utilizing knowledge and experience, a dependable esti-

[5] Robert Glen has contributed very materially to the ideas expressed in this section.

mate can be secured from a relatively very limited survey of probable egg-bed sites.

The same considerations hold with even greater force in estimating the abundance of ants which form large nests. Randomization there either fails completely of its objective, unless accompanied by conscious purposeful selection, or involves an immense amount of unnecessary work. In any event, it would give data with an unwarranted variability, since the range between the density of a "random" sample-unit which happened to fall in a nest and those which were situated far from nests would have no real significance for the particular purpose. A far better way is to study independently any recognizable areas of concentration and of scarcity, and then combine the data proportioned to the area each represents, to arrive at a general average for the whole community.

But while the instances cited are extreme they are not exceptional. In fact, with insects, it is the rule to have this type of distribution exhibited more or less strongly. Consequently the principle brought out has great force in all quantitative work relating to them. We are of the opinion that such work attains greater validity as well as greater efficiency if there is purposeful selection of sample placement wherever there is any sound knowledge upon which to base it. Use of the method (and formulae) of random sampling is predicated on the assumption that the population from which the sample (broad sense) is being drawn is homogeneous, i.e., that the variations within it are those due to chance. If this condition does not obtain, there is a cumulative error, which, however, can be reduced by suitable selective sampling.

Even when strict randomization is being practiced we suggest that it be done "systematically," e.g., by measurement, rather than by chance, in most instances. While personal bias is thereby at least equally reduced—this being an essential purpose of randomization—systematic placement of sample-units may in addition afford clues to important local factors influencing insect distribution. Thus, in work with wireworms it often serves to reveal spots, in an apparently homogeneous field, where populations tend to be maintained at higher or lower densities than the average; this in turn permits further study of the associated conditions, and often aids to develop an ability to pick out such spots by field inspection.

Exact or approximate duplication of sample-units of corresponding seasonal periods seems of definite advantage where work is being repeated at annual or other intervals. This procedure provides "paired" data, which often make possible more exact statistical analysis. In principle, too, this is analogous to the use of permanent quadrats in plant ecology. Care must of course be taken not to have the samples so closely spaced as to lead to progressive change of the whole sample area as the work proceeds.

With periodic or repetitive sampling, there is usually definite advantage also to duplicate as closely as possible the seasonal, weather and other eco-

logical conditions, at least for corresponding samples. At Saskatoon, the periodic sweeping is always done under relatively warm, clear, calm, noon conditions; while by early morning work it is possible to take most of the soil samples under conditions when few or no insects are active enough to escape. The latter of course is at times out of the question in hotter climates, but the principle is well worth working toward.

Consideration of a hypothetical problem may clarify some of the points that have been brought out. Let us say that the limitation of time only permits taking about one hundred square-foot samples, including adequate handling of the data; but that it is desired to gain some worthwhile knowledge of the soil insect population of a community, e.g., wheat fields, in a certain district for which only general information is available. "Complete" knowledge of a plot 10 x 10 feet could of course be gained by "sampling" all of it; but this would give no indication of how well the data represented average conditions. A much better way would be to take about thirty samples in a rather limited and apparently homogeneous portion of a carefully selected "typical" location, supplemented by some five to ten samples in each of several other representative fields; the thirty samples would permit fairly reliable statistical estimates of the populations of forms that are common and not too variable (cf. Jones, 1937), while the whole would provide a fair basis for appraising their variability and a reasonably good knowledge of the average for the season and district studied. For a different purpose, another good procedure would be to do the work periodically over three years, taking in one field some fifteen samples annually at intervals proportional to insect development and activity, with limited supplementary work in three or four other fields each year perhaps at periods which the data showed to be especially significant; in this way a better knowledge of "average" conditions would be gained and some idea of population trends with season and weather, but of course at the cost of having only very partial information of the condition at any one time and place. Each type of procedure serves a purpose, but obviously the first has only limited application and significance. On the other hand, complete lack of any "intensive" coverage is equally deplorable, at least until a solid background has been established by which to interpret limited work. Tentative efforts have been made (Fleming and Baker, 1936) to establish the percentage, of aggregate sample area to total plot or field area, required to give a reliable estimate of population. It seems evident that no set proportion can be established, except possibly for conditions that are definitely specified, e.g., as to area, species involved, and purpose in view.

Examining soil samples. Sifting or washing the soil are the two chief methods used for large-scale soil population study. These are often supplemented by a limited amount of special work such as direct examination, the use of Berlese or Lundgren funnels, flotation and centrifuging. As has been

indicated, exact standardization of the method of soil examination is probably not essential, provided that the approximate degree of accuracy is known and stated in each instance. This permits adaptation of methods to local conditions, particularly the character of the soil and its moisture content. Both main methods have the important advantage of permitting the use, under proper supervision, of semi-skilled labor to supplement the technical staff. While washing methods have an advantage in wet tenacious soil, our experience shows that there may be a considerable and variable loss of immature forms or other fragile material; it is also sometimes difficult to distinguish clearly, in the washed residues, between specimens that were alive and those that were dead prior to washing the soil.

Two distinct principles are represented in the several methods used for soil sifting. In one type, only those insects are counted that are retained within the sieves; this method has been used with success in the study of larger forms, such as certain wireworms (Lane and Shirck, 1928). In the other type, the sieve is used principally as a means of breaking up the soil and spreading it in successive thin layers that permit quick and accurate examination. For general soil insect population studies, or those which involve a considerable proportion of small material, we have found hand sieving, by the second principle, definitely superior both in accuracy and use of time, to any other procedure with which we are acquainted. It is realized, however, that this might not hold true under conditions widely different from those in Saskatchewan.

Supplementary methods. In one of the earliest population studies of any type (Decoppet, 1920, who cites data from 1841), systematic annual collections of white grub beetles were utilized as indicators of the localities involved and the probable severity of the subsequent outbreaks of the larvae; no actual sampling of soil appears to have been done, but the "forecast" of larval abundance, made on the basis of experience and close observation, seems to have been reasonably accurate. Rather similar methods, although with greater refinement and tested by detailed quantitative work with the soil stages, are being utilized today (G. H. Hammond, personal communication), in which a rapid survey of the area and severity of white grub outbreaks is made by systematic observation of the numbers of beetles feeding on trees or of the symptoms of such feeding; when appraised in conjunction with the knowledge acquired as to influence of soil types and plant cover upon place of oviposition, this permits a fairly detailed and accurate forecast of larval infestations.

Both light and bait traps have been used with considerable success for population studies of soil and other insects. Twenty years' use has shown that light traps have a definite value for measuring the abundance of economic cutworms, and as a guide to forecasting.[6] Estimates of the abundance

[6] Light traps have been continuously maintained, specifically for this purpose, for more than fifteen years, by the Lethbridge Alberta (H. L. Seamans) and Saskatoon laboratories. The writer was associated earlier with the work reported by Cook ('24).

of cutworm moths feeding on flowers have also proved useful (Cook, 1927, 1928).[7] By the empirical development of a powerful and more or less specific attrahent, bait traps are being used with extraordinary success in connection with the Japanese beetle (*Popillia japonica* Newman) as an indicator of populations as well as for partial control. Many other instances could be cited for both light and bait traps.

The chief weakness of bait traps for quantitative use is the difficulty of maintaining in a constant condition the substance used as an attrahent. Similarly, the power of attraction of light is not constant even for the same species, and the catch may also be affected by variable environmental factors. Moreover, it is an almost universal principle that these special population methods have only the validity which may be established by careful correlation with actual populations of the same or other stages of development. For example, there are very wide differences in the attractiveness of any light trap to different species. Hence each light trap must be, as it were, calibrated; and the data have a quantitative significance chiefly by comparison with the captures of the same species in other years.

In a somewhat similar way, it has been found possible to utilize the characteristic symptoms of the damage to wheat by wireworms as an indicator to permit the rapid but reasonably accurate survey of approximate categories of wireworm population. Such a development is of course based first of all upon quantitative work in the soil, and is only valid when the survey is conducted under comparable conditions, namely, during the critical seedling period of the first crop of wheat seeded after fallow. The method must also be constantly checked by comparison with the symptoms in fields of known wireworm population, and allowance made for differences in weather, soil, cultural and other factors.

In grasslands and similar habitats the sampling of the insect species and stages that are active above the surface or on the low vegetation is very intimately associated with soil population studies. While some progress has been made with other devices for this purpose, systematic sweeping with the insect net is still perhaps the chief reliance. Admittedly, this method has many shortcomings, one of the chief of which is the degree of influence of the personal factor in making the sweeps. Nevertheless, it is to be doubted if the results from carefully designed sweepings are quite so imperfect or relatively valueless as might be inferred from some of the critical statistical analyses of such data. It is probably true that exact comparisons by this method are only possible (Gray and Treloar, 1933) if a very large number of sweeps and samples are taken. Our experience (also see Carpenter, 1936, Carpenter and Ford, 1936), however, indicates that relatively few but periodic samples by this method do reflect at least the wider changes and differences that are found in these populations, and leads to the conviction that

[7] H. L. Seamans (personal communication) uses this method extensively to check the pale western cutworm forecasts, based originally on larval abundance and weather during the preceding spring.

the sweeping method is at least decidedly superior to mere observation or visual estimate.

Other points. It will be noted that while most of the methods described give an actual census of insects, some of them are intended only to indicate approximate categories of population. The latter however are, if dependable, usually quite adequate for forecasting of outbreaks. In any case the severity of outbreak depends in considerable part upon future weather, a factor which is at present unpredictable. The "ratings" can, however, make allowance for other important local factors such as soil; our experience in Saskatchewan shows that it requires approximately twice the egg infestation in heavy clays as in light sandy soils to give the same "outbreak" expectancy for the "stubble" grasshopper (*Melanoplus mexicanus* Saussure).

In the interpretation and comparison of population data, especially those secured by sampling periodically through the season, adjustment must be made for the periods of occurrence and of activity of the different constituents. This is especially true where certain developmental stages do not occur in the soil, or are too small to be found with accuracy. Some kinds, such as wireworms, will be taken throughout the year, although possibly only active for a period no greater than that of other forms, such as cutworms, which are only represented in the samples during a limited season. Approximate methods of weighting the data for various types of seasonal occurrence may have to be worked out to meet such differences.

Finally, soil population studies can only be successful on a sound taxonomic basis. This involves close collaboration with taxonomists who are willing to take an interest in this type of work although it tends to yield material that they find rather unsatisfactory. The viewpoints of the taxonomist and the ecologist are often divergent, in that the former tends to be interested chiefly in species, especially the rarer ones, while the latter is much more concerned with abundance. Many population investigators fail to do their part, however, in that their material is obtained and submitted in a much poorer condition than it need be, and too little preparatory work is done, thus making the work of taxonomists unnecessarily difficult. On the other hand, the taxonomist might well make allowance for the fact that much of the material obtained is, unavoidably, in rather poor condition. There is great need for more specific and reliable identification of the insects found in population studies, especially of the immature stages. The ecologist should be one of the strongest supporters of sound taxonomic work.

DISCUSSION

There remains to indicate a few of the results obtained from soil insect population studies, approached particularly from the viewpoint of appraising something of the potentialities of the method. At best, at this stage of research progress appraisal can only be preliminary, since developments in this field

are so recent and relatively so little has been accomplished even yet. The development of better quantitative methods, which is one of the first important results of population studies, leading to still better and more significant work, has already been discussed.

Interestingly enough, while considerable stress has been laid upon the ultimate practical application of results of studies in so-called pure science, it has perhaps not been equally realized that information having a broadly scientific bearing can be, as it were, a by-product of sound "economic" studies. Other things being equal, why cannot data of "purely" scientific value be gained from the study of an insect of economic importance just as well as if it dealt solely with non-economic forms? The project would thus gain a double ground for support. It seems to be largely a matter of planning, and with this in mind would it not be well to work in some population study dealing with the whole community, as a part of the field investigation in each economic problem? Unquestionably, such procedure would react ultimately to great practical advantage as well as to the general progress of the science.

These thoughts have arisen in part from a consideration of the grasshopper surveys conducted in recent years over the entire Great Plains area. In 1938, nearly fifty thousand soil samples were examined for this purpose in Saskatchewan alone. If all of the quantitative work on this project in the Great Plains area both in this and preceding years were included, this figure would be multiplied many times over. It would be quite impractical to duplicate this immense amount of data for any insect not of great economic importance. The data have, of course, already been used to advantage not only for the preparation of forecasts but also for the development of more rapid and accurate survey methods. Yet it seems to me that here we have an opportunity to study, on an unprecedented scale, the population distribution of a common and characteristic insect form, and that from broad analyses of such data there could be built up sound generalizations, which would illuminate the whole question of distribution of soil and surface insects.

Climatic relations. A very great opportunity steadily to deepen and broaden our knowledge of the relation of climate and weather to insect abundance is afforded by population studies, particularly of soil insects and in grasslands and similar communities. While this is especially true of general studies, important contributions will also be made by work with individual species or limited groups. Light is thrown upon these relations by a study of the results from comparable work in widely different regions and climates, in different communities or micro-climates within the same region, and particularly in the year-to-year comparison permitted by long-term investigations in the same community.

Such research will gradually make possible better appraisals of the ecological homogeneity or diversity of taxonomic groups, large and small. At Saskatoon, even when an exceptionally dry year followed the exceptionally

wet summer of 1923, the several constituents of some taxonomic groups exhibited very diverse reactions to these strongly contrasting weather conditions. On the other hand, the immature soil Diptera group was more than three times as numerous during the wet season than it was during and following the dry one. The same general tendency of immature Diptera seems to be shown by the fact that they are relatively abundant in aquatic communities, in moister climates (e.g., Great Britain vs. Saskatchewan), in the moister habitats or micro-climates of the Saskatoon district, and during the moister seasonal periods of the year (autumn, winter and spring in most northern climates).

Great care must of course be exercised not to draw conclusions as to taxonomic group reactions where there is really a domination by a few abundant species (cf. Ford, 1938), and to distinguish between variations resulting from environmental differences and those due to life-history. Then, too, it may well be found that the adults of a group may show quite a different response to climatic factors than do the immature forms. In any case a great deal of work will be necessary before valid generalizations can be drawn even for a group which seems as relatively homogeneous as do immature soil Diptera in their reaction to the soil moisture factor. Even then, no doubt, important exceptions will be found, although these may throw equally important light upon the conditions governing such reactions.

Nevertheless, attempts in this direction may help to overcome the serious handicap to which all entomological work is subject, namely, the tremendous number of insect species. Because of it, work which stresses similarities instead of differences, and permits valid grouping of species for certain purposes, seems fully as worthwhile as are studies designed to bring into sharp contrast specific diversities. Synthesis is often as essential as analysis. Well-designed population studies will, we believe, permit increasingly broad and valid generalizations to be drawn in this way, which in turn will serve as valuable guides to both economic and general work.

Another worthwhile development to which population studies can lead, we believe—though only after our knowledge has vastly increased—is the use of certain insects as highly sensitive indicators of changes in environmental conditions. While plant indicators have been used to good advantage (Clements, 1920), in most instances they seem to serve mainly to show changes that have already progressed to such an advanced stage, as respects the plant constituents of the community, that reversal and restoration are difficult and slow. It is believed that insect indicators, on the contrary, because of their short life-history and consequent ability to react rapidly to environmental differences, can eventually be used to forecast changes which would take place were the critical conditions not speedily rectified. It is suggested that such criteria, when established, will have an important relation to the problems of conservation, among others, permitting pre-

ventive measures to be taken before the adverse effects have advanced too far. The same principle applies to many other economic studies, such as in agriculture, where quantitative work may give warning of the development of potential pests. The best insect "indicators" will not necessarily be the predominant species, for which reason ecological and other quantitative studies should not neglect the less abundant forms.

Community relations. Although soil insects constitute only a part of a community, quantitative study of them contributes to an understanding of the community as a whole. Ecology deals primarily with the forms that are predominant, as measured by size, frequency and interactions. Obviously, insect importance must lie in the two latter factors. With plants and the larger animals, it is the dominant species that are commonly dealt with, and from which communities are named. It is suggested that with insects, because of the large number of species, this procedure is not necessarily valid. Instead, a number of species may have to be considered as together constituting a "predominant" group. Such groupings would not necessarily be taxonomic ones but would include those species whose action is similar or supplementary in its impact upon the community as a whole. Thus, a number of abundant insect forms, all acting against certain plants to the advantage of others, may influence a community fully as much as does a single abundant species of large animal, or a plant "dominant."

Viewed in this way, grasshoppers may properly be considered to be one of the predominant forms of the Great Plains grasslands, as typical and in many ways perhaps as influential, as the buffalo. Grasshoppers of course fluctuate very widely in numbers and influence, but outbreaks still return periodically while the larger native grass feeders have disappeared as a factor of importance. The true relations of grass-feeding insects to the community are not easy to measure, but the validity of the suggestion made is already supported by some significant studies (Morton, 1936, Treherne and Buckell, 1924, Wolcott, 1937).

While the abundance of insects is a large factor in determining their ecological "niche," their interactions with the community are probably still more significant, and more difficult to measure. One type of interaction is found in the insect-born diseases. Another is the way in which the insect factor is associated with drouth effects and other climatic influences, which often seem to act on plants as much through the agency of the insects which they favor, as they do directly. Allied to this is the effect of insects at transition zones, where they may materially modify climatic or soil influences. In the economic field, it is known that insect pests may force the abandonment of certain crops in localities otherwise fairly well suited to them. But in native communities this field is still largely to be explored, especially in relation to soil insects; and it is doubtful if it is valid to assume that the relative effects are less, merely because there they are more stabilized.

The importance of insect attack depends in part on whether it comes at a critical place or growth-stage of the plant. For example, spring wheat is particularly subject to damage by our prairie wireworm, because their maximum activity is directed to an attack on the seed and growing point of the seedling where resistance is low. Such occurrences in pest studies suggest the possibility of similar interactions in native communities. Attacks of this type may exert an important differential in favor of perennials over annual species, materially contributing to the general predominance of the former in most native communities.

Soil insect pests. Some of the possibilities suggested in this discussion, it must be owned, are still largely or partly theoretical. But that is not true of the solid accomplishments to which population studies are contributing in respect to soil insect pests. With insects that live above the ground, a fairly accurate estimate of their numbers is often possible by keen observation, and sometimes from visible damage. With species that work in the soil, however, such methods meet with much greater difficulty, and it is seldom possible to arrive at any valid estimate of numbers without quantitative methods. The natural tendency with soil pests, therefore (when work was unavoidably limited), has been to assume that their numbers are completely correlated with the indirect symptoms of damage. Population studies of soil insects, however, are showing that this is very far from being a valid assumption. The use of quantitative methods, enlightened by this concept of "infestation versus damage," are proving of increasing value in economic studies because they permit the adequate testing of all details of methods proposed for reducing either infestation or damage. Such testing is especially important for soil-pest control, which must usually be accomplished by indirect means. Population studies are throwing new and important light on many of these stubborn problems, and permitting increasing progress towards their practical solution.

Of great economic importance is the ability to forecast insect outbreaks accurately. Reliable forecasts make it possible to warn the agricultural public, to make campaign preparations and to effect timely alterations in farming practices and the use of crops, all of which contribute to more complete and more economical control. Both the original development and the annual continuation of valid forecasting are almost completely dependent upon population studies. In some instances, as in forecasting for the pale western cutworm (Seamans, 1923), it has been found possible to utilize a knowledge of weather factors to project a probable abundance curve some time into the future. Eventually, however, such work depends upon a knowledge of actual or relative numbers at some period and place.

Population studies can also throw important light on activity, life-histories, seasonal variations, and other phenomena of practical importance, which otherwise are very difficult to study in the soil under anything approaching natural conditions.

CONCLUSION

Even from this incomplete and often superficial review, and still more from any detailed appraisal of the work already carried through, it is evident that population studies afford a procedure of very great practical and scientific potentiality, if properly utilized. This is perhaps particularly true in relation to soil insects, and in certain types of communities such as grassland (Hanson and Vorhies, 1937).

The method of course is not "foolproof." The two main criticisms commonly, and often justly, made of population studies are, first, that they tend to stop with the mere accumulation of masses of undigested data, and second, that often they are not sufficiently rounded out by laboratory experimentation. It is pertinent to point out, however, that such defects are by no means limited to those who employ this particular technique. In all lines of study there are workers who are greatly handicapped by unwillingness or inability to correlate and fully utilize the data secured. The effects of this are of course most pronounced in work which yields abundant data. Laboratory workers, however, have perhaps the greater tendency to become one-sided or "narrow." As a matter of fact, the two phases, field study and laboratory experimentation, are truly complementary and should develop hand in hand in all projects. It is to be doubted if really sound laboratory work is possible in either biology or agriculture unless the worker possesses and maintains an intimate personal acquaintance with field conditions—he must "keep his feet on the ground," both literally and figuratively. Conversely, the soundest and most productive field work is rarely possible unless the "leads" thus gained are utilized for the planning of laboratory experiments by which the conclusions may be further tested, and new means thereby suggested for reattacking the problem and for reinterpreting and reanalyzing the field data.

Apart from whatever direct results may be secured from population studies, they justify some attention from each student and young worker, if only for the aid the method and viewpoint give to his own development. This effect has often been observed. Once an investigator has endeavored to deal quantitatively with insect populations, and to interpret the results in relation to all elements of the environment, it is almost impossible for him ever completely to lose this broader viewpoint or to become specialized to an undesirably narrow degree.

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POPULATIONS OF SOCIAL INSECTS[1]

By

ALFRED E. EMERSON

Department of Zoology, University of Chicago

It is my function in this symposium briefly to outline some of the factors influencing the biology of the populations of social insects. Inasmuch as the social insects differ from other insects in their more complex integrated populations, it would seem to me that my discussion should place some emphasis upon the complexity of the population dynamics characteristic of these forms.

At the same time, the factors which influence population biology of social insects may also play an important role at various other levels of population integration. We may thus be able to give hints to the investigator of simpler population systems, much as the vertebrate physiologist may suggest interactions occurring in the protozoan.

To what extent the biology of populations of social insects may help in the understanding of human populations is as yet not clear (see Hogben, 1931). Pearl and Gould (1936, p. 418) state that "the tendency of human social organization to approach more and more closely that of the termites has been evident for a century at least; with its increasing rigid differentiation of occupational castes, its abrogations of individual liberty of action, its heavy and ever-growing burden of economic overhead service expense entailed in getting subsistence; all these being direct consequences of living under conditions of high population density." The least one can say is that the effect of social organization on population dynamics of all available social animals is an important problem which demands careful investigation.

In spite of the obvious complexity of the interacting factors influencing the social insect population, I have attempted to make a simplified diagram which will illustrate some of the major factors and the direction of their effect (Figure 1). Surrounding the central population complex are arranged in concentric circles (1) the intraspecific societal factors, (2) the interspecific societal factors, and (3) the environmental factors, both physical and biotic. All these factors are divided radially into those which tend to increase the population, those which tend to decrease the population, and those which fluctuate in their effect upon increase or decrease of the numbers and types of individuals.

The direction of the effect of each factor is indicated by the arrows. The arrows are pointed in both directions if there is a reciprocal interaction

[1] I am indebted to Dr. W. C. Allee and to Dr. Thomas Park for many helpful suggestions.

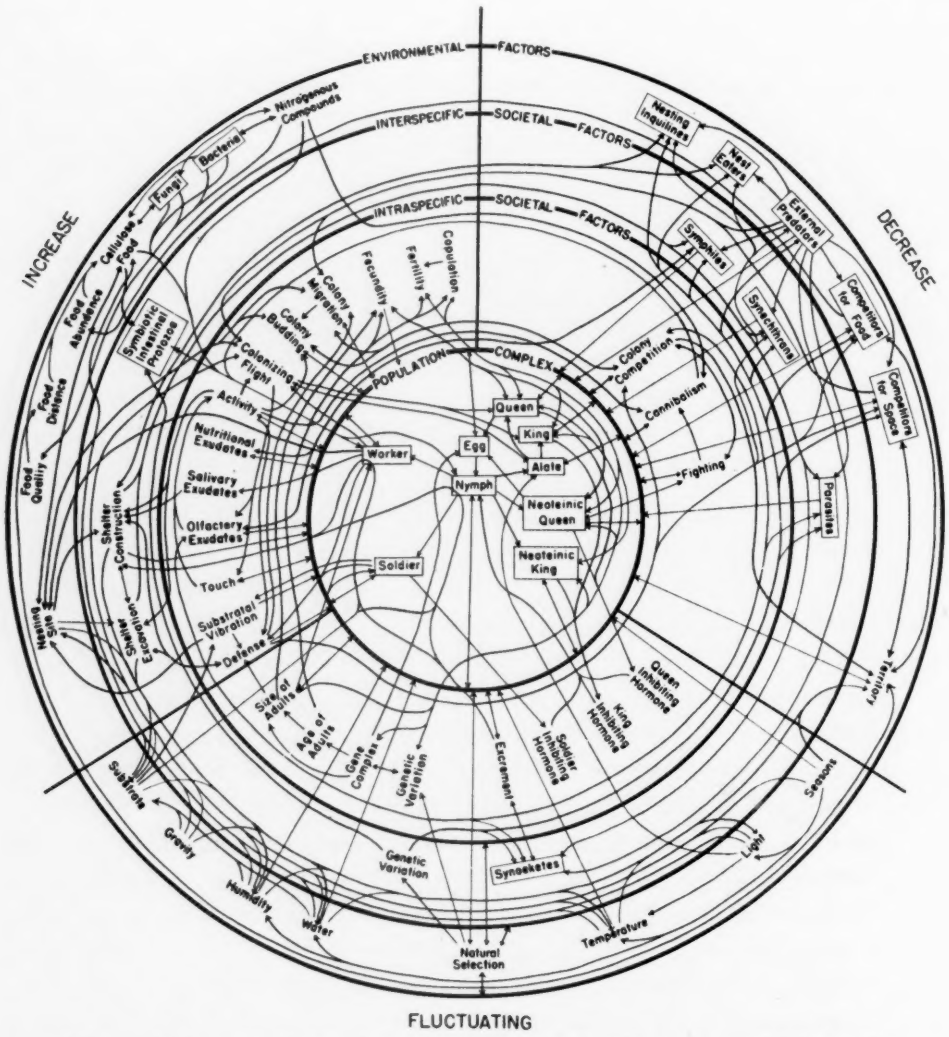

FIG. 1.—Diagram of the factoral complex influencing the population of a typical termite of the family Rhinotermitidae. Arrows indicate the direction of the effect.

between the factors. Organisms are boxed in order to distinguish them from other factors.

Theoretically, each of these arrows could be evaluated quantitatively and a thorough knowledge of any such population would have to rest upon quantitative comparisons. So far, students of social insects have contributed meager information concerning the quantitative dynamics of the populations they have been studying. It becomes increasingly apparent that this is a rich field for future investigation.

The diagram is supposed to indicate the factoral interrelationships in a population of a more or less typical species of termite belonging to the family Rhinotermitidae. It would be possible to make a series of diagrams illustrating various groups of social insects. Time did not permit such

an undertaking, but even a brief consideration of the possibilities indicates that genera, tribes, subfamilies and families would show striking qualitative and quantitative differences among the population factors. Often the species of a single genus would show considerable differences in their respective diagrams, but the majority of the specific differences would probably be variations in the degree of influence of certain factors (Talbot, 1934).

It should be emphasized that population growth and periodic fluctuations involve quantitative variations in the influence of many factors, so a static diagram is hardly more than a single frame in a motion picture reel. The population growth of single colonies of various social insects follows the logistic curve (Bodenheimer, 1937), and such population changes could only be expressed through successive quantitative evaluation of the forces operating on the population numbers.

The logistic curve is the result of an increasingly severe environmental resistance counteracting the potential geometric production of numbers of individuals (Pearl, 1930b; Smith, 1935; Park, 1939). Stabilization of the population near the upper asymptote occurs when these two tendencies balance each other. In non-social species, the initial population produces more individuals with reproductive capacity, while colony growth in the social insects is due to the increase in the productivity of a single queen (usually) through the feeding and care by her sterile offspring. The problem of population growth as measured by the number of colonies should be similar to that found in non-social species.

It will be impossible in the time at my disposal to deal with more than a few of the population factors outlined in the diagram, and many other factors would have to be mentioned in order to give even a brief analysis of the populations of the more important types of social insects. I shall therefore confine my remarks to a selected series which illustrate various interesting effects.

Social insects are particularly distinguished by the different castes which make up the populations (except in the case of social parasites). We are thus dealing with an extremely heterogeneous population. Most of the careful quantitative studies of insect populations have dealt with relatively homogeneous populations. In the social insects we have the complexities of stages in the life cycle (Nelson and Sturtevant, 1924) and sex differentiation, and in addition must deal with a variety of adult types with striking variation in their population influence (see Nolan, 1925; Schneirla, 1938; Morland, 1930).

A single egg-laying queen is typical for most colonies of social Hymenoptera, but considerable variation may occur, particularly in such nests as those of *Formica exsectoides* which adopt impregnated females after the mating flight. Cory and Haviland (1938) found 1,407 queens in one nest of this species with 168.5 workers for each queen.

In the majority of termite nests, a single pair of primary reproductives occurs without neoteinic reproductives, but occasionally one may find two queens with a single king, two kings with a single queen, or other variations in numbers. Very rarely one may find a great many primary reproductives in a single colony, usually because of the lack of nesting sites (Emerson, 1933). If neoteinic reproductives occur in the colony, there is usually a number present (Emerson, 1933).

The tendency to confine reproductive activities to a single female impregnated by a single male is found in all social insects and has an important influence upon the character of population growth (Bodenheimer, 1938, p. 78) and the evolution of the population complex. Weismann (1893, p. 327) made the following significant comment:

> Were many females of a hive engaged at one time in the production of eggs, the natural selection that depends on the quality of the brood of workers brought forth would be far more difficult and much slower, inasmuch as the prosperity of the hive would depend on many differently constituted workers, and so, in some measure, only the resultant of the produce of all these females would be selected: a queen would by no means be doomed to extinction because she had produced a bad race of workers, for her hive would at the same time be provided with a brood of workers by other queens, and if the majority of these produced better workers, the hive would perhaps hold their own against others in the struggle for existence for a long time, till at last the worser worker-brood distinctly preponderated in the hive. . . . I could almost suppose that the remarkable reduction of the fertile females to a few or only one has taken place because the gradual improvement of the sexless by natural selection can thus to some extent proceed more easily and more rapidly; or rather, the hives with few queens had an advantage, because they could improve themselves relatively more quickly.

Snell (1932) points out that the mating flight in the social Hymenoptera selects fit males. In haploid males, the phenotype and the genotype are the same. The female progeny from a single mating are identical in at least one-half their germ plasm, because only one kind of sperm is produced.

Fecundity has become a prime factor in the evolution of the division of labor among the social insects. The queens of the more primitive social insects do not lay many eggs per day. A wasp queen has been recorded laying 10 eggs per day and many of the mature queens of primitive bees, ants and termites do not lay more eggs (Kalshoven, 1930), even during the height of the season. The fecundity of the more specialized social insects, however, has been developed enormously (Eckert, 1937). An ant queen has been recorded laying 341 eggs per day; 3,021 eggs per day has been counted for a honeybee queen; and a capacity of 6,000-7,000 eggs per day is not unusual for specialized termite queens which may live from 15-50 years.

There is an apparent correlation of fecundity and certain taxonomic categories, giving evidence that there has been an evolutionary tendency to increase the egg-laying capacity of the queen. This hereditary capacity is also

correlated with evolutionary adjustments of social coordination and environmental control. Great fecundity is therefore correlated with high social efficiency and large population numbers.

These eugenic mechanisms probably offer us a basis for understanding much of the special character of the social insect population and also show us the necessity for considering the whole colony as the unit upon which natural selection is acting.

The determination of the castes of social insects has been an interesting problem for investigation since ancient times (Hare, 1934). Only recently have techniques been devised which give hope for the solution of this difficult problem. The experiments are by no means final at the present time, but are suggestive. Castle (1934a, 1934b) and Light (1934) have shown that the reproductive castes and the soldiers give off exudates containing inhibiting substances. These substances are passed to the nymphs through the exchange of exudates (trophallaxis) within the colony (Wheeler, 1918). Experiments removing the queen from colonies containing numerous nymphs of various instars show that a new neoteinic queen is produced in 35-50 days. Alcohol or ether extracts from queens, when fed on filter paper to similar colonies, significantly delay the production of a new queen. The production of kings and soldiers from undifferentiated nymphs is indicated by similar experiments with these castes. The soldiers thus tend to inhibit other soldiers from developing, kings inhibit other kings from developing, and queens inhibit the development of other queens. The proportional representation of the castes in the population thus seems to be regulated by this hormone mechanism. The percentage of soldiers in various species of termites with workers runs from 3 per cent to 16 per cent of the sterile castes. At points of disturbance, the soldiers may congregate out of proportion to their actual representation in the entire colony.

The periodicity of the production of alates may also be explained through such chemical coordinating agents (Emerson, 1939). Seasonally, large numbers of alates may be found. Holdaway, Gay and Greaves (1935) report 2.4 per cent alates in a colony of *Nasutitermes (=Eutermes) exitiosus* (44,000 out of 1,806,500).

It has long been known that food differences are correlated with the determination of worker and queen castes in honeybees. Secretions in the royal jelly and in the bee bread may contain coenzymes which, when activated, control development of the castes.

The case of ants has yet to be adequately investigated (Whiting, 1938), although preliminary experiments by Robert Gregg suggest a similar mechanism in ants to that in termites.

Cannibalism may be considered as an intraspecific societal factor which decreases the population and plays an important role in the population dynamics of ants and termites. In the process of founding new colonies, both ant

and termite reproductives have limited powers of foraging. Wheeler (1933) shows that the most primitive ant queens forage during the early development of the new colony and colonizing reproductives of termites are also known to eat some wood and feed the nymphs which develop into dwarf adult soldiers and workers. In the majority of instances, however, many of the eggs and young are eaten by their parents. Cannibalism is also probably characteristic of the mature colonies of ants and termites, even under optimum conditions. Cook and Scott (1933, p. 104) and Hendee (1934, p. 316) have shown that termites deprived of nitrogenous food show an increase in cannibalism. Injury of a termite will often result in its being eaten by workers. If only slightly injured, an active termite may avoid being eaten until the wound is healed (Emerson, 1933).

To what extent cannibalism may be considered beneficial to the colony is a question. Snell (1932) suggests that it has eugenic significance in the termite colony, but certainly the vast majority of cases are of no importance in controlling the composition of the gene complex of the reproductive castes. Rather, cannibalism seems to conserve valuable products that might otherwise be lost. There is also a possibility that cannibalism partially controls the proportions of the castes in the population. This has by no means been proved experimentally for ants and termites, but the action of bees in destroying excess queens and drones, although not cannibalistic, nevertheless indicates that population control is part of the behavior pattern in at least some of the social insects.

The food adjustments of the social insects vary considerably and it may be possible to draw generalizations from the comparison of the food influences upon the populations of these insects. The social Hymenoptera originated along several lines from solitary predacious wasps and most of the social wasps and primitive ants retain this feeding behavior. Many of the ants have become scavengers, while others have evolved adaptations to special food such as the honey dew of aphids, and one tribe cultivates fungus. Some of the most interesting adjustments of ants are to be found among the thief ants, slave-making ants, and the social parasites, with consequent specialization or loss of their sterile castes. The bees have become specialized pollen and nectar feeders. Termites, originating from wood-eating roaches, are specialized cellulose feeders. The more primitive termites depend upon symbiotic flagellates for the digestion of cellulose, but the more numerous populations of specialized termites (Termitidae) have lost their dependence upon intestinal protozoan symbionts. The physiology of cellulose digestion in these more highly evolved termites has not as yet been investigated. There seems to be a general tendency for the population numbers in the colony to become larger in the vegetarian and scavenger types of social insects, and to become smaller in those which have evolved cleptobiotic, lestobiotic, slave-making, or social parasitic behavior, while the population size of the colonies of the predatory species is roughly between that of these other feeding types.

External predatism is an extremely important factor in diminishing the population of social insects and doubtless is the factor which has directed the evolution of the effective defensive adaptations. The sting was an offensive weapon in the ancestral solitary wasps which gave rise to the social wasps, bees, and ants, and in many instances, these social Hymenoptera still use their sting for offense as well as defense. Other forms of defense, such as biting and the acid sprays of certain ants, are also used for attacking prey. One cannot say that the evolution of the soldier ant from polymorphic workers is merely an adjustment to defense against predators, even though the soldier of the fungus-growing ants *(Atta)* would seem to be purely defensive. The soldier termite, however, is clearly an adaptation for defense against external predators and other factors are of minor influence in the evolution of this caste. The evidence is clear that the soldier was the first sterile caste to evolve among termites and that adult workers evolved much later (Emerson, 1926). Different types of defense, such as biting, toxic gas, and viscid ejaculations, are found among termites and it is probable that the soldier defense adaptations are of great importance in the biological success of certain termites such as the genus *Nasutitermes.* It is interesting to note, in this connection, that the more primitive genera of the Nasutitermitinae (*Syntermes, Labiotermes, Cornitermes, Armitermes, Curvitermes,* and *Rhynchotermes*) with mandibulate soldiers are all confined to tropical America, while the later evolved genera containing nasute soldiers (*Nasutitermes, etc.*), with degenerate mandibles and a well-developed apparatus for ejecting a viscid liquid upon their enemies, have spread to all tropical regions. The biological success of those termites with the nasute soldier is doubtless influenced by other factors as well as defense against predatory enemies, but the efficient defensive adaptation against external predators seems to be the most important single influence.

It is also fairly obvious that the arboreal nests of some species of *Nasutitermes* have been important factors in guiding the adaptive evolution of the prehensile-tailed anteaters and pangolins, which have evolved methods of overcoming the defensive adjustments of the nasute soldier. These arboreal termite-eating mammals retain fossorial forefeet, a unique combination of adaptations which can only be understood through their specialized food adjustments. Reciprocal adaptive evolution of the predator and prey contribute to a moving biological equilibrium (see Nicholson, 1933, for opposing view), but the tendency to equilibrate populations during long evolutionary history does not mean that predator-prey relationships are not determining major evolutionary changes through strong selective forces.

The accumulation of excrement would usually be considered a factor contributing to the decrease of the population, but among termites excrement is turned to a certain extent into a factor of increase through the construction behavior of the workers and larger nymphs which use excrement for nest

material and mortar. The cooperative construction behavior enables these insects to control or avoid important factors of the nesting site and territory such as soil water, rain water and a dry atmosphere. One is forced to the conclusion that cooperative control of optimal environmental conditions for the organisms composing the society is an important directional tendency in the evolution of the social insects, much as the cooperative control of optimal environmental conditions for the cells of a multicellular organism is an important directional tendency in the evolution of multicellular organisms (Emerson, 1939).

Although excrement does not play much of a role in nest construction among the social Hymenoptera, cooperative shelter construction is characteristic of most of the social insects. The pattern of behavior resulting in nest construction is clearly the reaction of hereditary physiological and nervous mechanisms to intraspecific and environmental factors (Chen, 1937a, 1937b; Combes, 1937; Emerson, 1938, 1939).

The nests of social insects help the population to avoid sharp climatic changes, such as storms and changes in temperature and humidity (see Dunham, 1930, 1931), as well as affording shelter from many predacious animals. Natural shelters are often converted into more adequate shelters through excavation, and constructions often enable these insects to invade regions which would be otherwise uninhabitable.

Dr. K. M. King has just given an interesting discussion of the populations of soil insects. Many termites should certainly have to be included as soil insects and are known to be important organisms contributing to the soil characteristics, particularly in the tropics. With little physiological evolution, however, some of these soil termites have invaded the tops of the forest trees by the simple process of establishing their soil environment in the tree tops. Here they construct dirt nests (*Amitermes excellens, Microcerotermes arboreus,* etc.) at any height above the ground with covered dirt tunnels connecting with the ground. Shelter from rain and from many predacious enemies, together with the maintenance of the high humidity characteristic of the soil environment, are advantages maintained by these arboreal populations.

The great majority of the species of the termite families Rhinotermitidae and Termitidae are highly sensitive to the evaporation power of air and could not live for long in a dry atmosphere. Nevertheless many species of these termites inhabit desert regions and this seemingly contradictory distribution is due to their ability to construct tunnels and chambers in which a high humidity is maintained. The natural advantages of the soil environment are augmented by many of the social insects through the nest-building activities of the cooperating population. The mound nests of many ants and termites enable these insects to survive excessive soil water. Some termite mounds are also adapted to shed rain water and to regulate temperature (Emerson,

1938). Such activities of populations are among the best to illustrate the biological advantage of social cooperation.

The ability of social insects to regulate their environment enables the populations to remain relatively stable under external environmental fluctuations (see Elton, 1924, 1927). Sudden large increases and decreases of populations are not, therefore, generally characteristic of social insects, except in the few instances of introduction by man into new and favorable environments. Large periodic fluctuations of the total population of tropical species are not very striking. In temperate regions, the populations fluctuate with the temperature as is characteristic of poikilothermic animals. There is less fluctuation in the case of the soil species than with the more exposed types in which the sterile castes may not survive the winter season.

The evidence points to the conclusion that the adaptive evolution of dynamic integration of the population components of social insects can only be explained through the natural selection of the entire population unit. Such a coordinated population may be considered to be a superorganism and many principles applying to the individual organism find expression in this superorganismic individual (Wheeler, 1911; Emerson, 1939). The colony unit with neoteinic reproductives may be potentially immortal (Light, 1934, p. 41). A colony of *Neotermes castaneus* was kept by Father F. L. Odenbach and the author in a flask for 24 years and finally died by accident. Bodenheimer (1937) gives the contrary opinion that a natural senescence of the colony seems to be normal not only for termites but for all other types of social insects.

In varying degrees, many of the dynamic factors which coordinate social populations also operate at simpler population levels such as the family unit, the sexual pair, and other types of organized animal aggregations (Allee, 1931; Park, 1939). We seem to be forced to the conclusion that adaptive integration is largely due to the natural selection of these various whole population units (Weismann, 1893; Marshall, 1936; Sturtevant, 1938; Emerson, 1939). The individual organism is not the only unit upon which natural selection acts (see Pearl, 1930a). Thus, cooperative population systems are natural biological units and not merely human concepts based upon statistical summations and formulae (Pearl, 1937; Park, 1939). The student of population biology, therefore, is attempting to analyze and synthesize objectively real units.

Other papers in this symposium give evidence that a knowledge of the factors controlling the population dynamics may often lead us to methods of controlling populations in which we may have an economic interest. Knowledge of social mechanisms such as trophallaxis and cannibalism has led us to methods for the control of pests among the social insects.

Information on the total population of any social insect per unit of area is very meager and generalizations and comparisons are still bound to rest

on inadequate data. Recently Cory and Haviland (1938) have estimated about 12 million individuals of *Formica exsectoides* per acre in a 10-acre plot in Maryland. (Also see Andrews, 1929; Carey and Diver, 1937; Dreyer and Park, 1932; Forbes, 1938; Holmquist, 1928; Nefedov, 1930; Nelmes, 1938; Pickles, 1935, 1936, 1937; Weber, 1935.)

In the case of ant populations, density has been expressed by Elton (1932) and Pickles (1938) under three categories. *Lowest density* is the total population divided by the area of the census; *economic density* is the total population divided by the territory actually occupied; *greatest density* is the population of the nest at night. In his studies of the populations of three species (3 genera) of Yorkshire ants, Pickles (1938) shows that the species *(Acanthomyops flavus)* with the smallest territory per nest (3.14 sq. yd.) had the largest economic density (352.149 per sq. yd.), the largest lowest density (4.204 per sq. yd.), and the smallest weight per square meter (0.003 grams); while the species *(Formica fusca)* with the largest territory per nest (236.00 sq. yd.) had the smallest economic density (2.118 per sq. yd.), the smallest lowest density (1.425 per sq. yd.), and the largest weight per square meter (0.006 grams). Whether such proportional tendencies will hold true for other species in other regions has yet to be determined, but in any case such detailed population studies will certainly add much to our understanding of population dynamics. It is hoped that quantitative data on the total populations of social insects in a variety of ecological habitats may be collected in the near future.

Population dynamics is not confined to the intraspecific population. I think that the diagram (Fig. 1) of the factoral forces influencing the population of a typical termite colony indicates that it is fairly difficult to separate the intraspecific complex from the interspecific complex. Probably the best illustration of interspecific integration is to be found in the symbiotic relationship of the intestinal protozoa with their termite hosts, largely understood through the splendid experiments of Cleveland (1923a, 1923b, 1924, 1925a, 1925b, 1925c, 1926, 1928, 1934). Cleveland (1934, p. 209) has shown that colony life is essential in the primitive termites because the symbiotic protozoa are lost at each molt and reinfection can only occur through association with non-molting individuals (see Emerson, 1939). The mutual adaptive interspecific cooperation of these diverse animal populations can only be explained through the action of natural selection on the interspecific unit. Thus we find population biology merging with community ecology.

Bodenheimer (1938, p. 142) states that small integrated monospecific communities may reach a true superorganismic structure, but that superorganismic integration between the members of a biotic community is extremely rare. Although superorganismic cooperative integration seems to play only a minor role in the larger communities, it would seem that interspecific population systems are sometimes selected as units and may thus be

considered as objectively real entities. Competition and toleration rather than cooperation may be the prime factors in community organization (Nicholson and Bailey, 1935), but there seems little doubt that such cooperative relations as the insects and flowering plants (Robertson, 1928; Pearson, 1933) and seed dispersal by animals, as well as other cooperative activities (Allee, 1938), have had an important influence in the evolution and maintenance of large biotic communities.

In closing, I find it necessary to state that the person who attempts to make even a brief and inadequate summary of some of the factors contributing to the complex populations of social insects is bound to be impressed by the superficial state of our knowledge at the present time. Quantitative studies are extremely few and doubtless many important qualitative factors remain to be discovered by the student of the intimate behavior and population physiology of the social insects. It is my hope that this paper may help in a small way to stimulate such investigations.

SUMMARY

The complex interrelationship of factors having an effect upon the population dynamics of social insects is diagrammed and discussed. The factors influencing the population complex are divided into the intraspecific societal factors, the interspecific societal factors, and the environmental factors, both physical and biotic. All these factors are divided into those tending to increase the population, those tending to decrease the population, and those with a fluctuating influence upon numbers. Among the many factors, emphasis is placed upon social hormones, fecundity, cannibalism, types of food, predatism, nest-building, and environmental control. The integrated population unit is regarded as the result of natural selection acting upon the group as a whole. Both intraspecific and interspecific groups are considered as objectively real biological units.

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FOREST INSECT POPULATIONS

By

SAMUEL A. GRAHAM

University of Michigan

Most workers on population problems are impressed with the complexities of these problems. Nevertheless when we examine the results of the reactions between the various forces acting upon a population, we cannot but marvel at the consistency of the end result. This interaction of forces invariably results finally in an equilibrium that fluctuates about a definite mean so that on the average each individual in one generation is replaced by another individual in the next. It is obvious that such a condition must be characteristic of populations, otherwise animals would more frequently either become extinct or come to dominate their environment at the expense of other forms of life.

This end seems so obvious and consistent that it must be controlled by the action of some simple law or laws. Perhaps the complexities that perplex us when we consider populations arise because we are chiefly concerned with disturbed conditions and restless populations seeking equilibrium, like the surface of the sea after the hurricane. The waves rise and fall, each acting upon the other adjacent waves, and each affected by invisible currents until the position or even the existence of a mean level is obscured.

Man has been the great disturber of populations, and unwittingly has set in motion forces that he neither understands nor can control, forces that may ultimately result in his destruction unless he finally learns to understand and conform to them.

Man's activities are continually affecting the orderly arrangement of nature, first in one direction and then in another. Primitive forests are replaced by corn and wheat fields, followed by soil depletion, erosion, and abandonment. Wild animals are replaced by domestic stock, and native forage by weeds. Insects and fungous pests attack man's crops and man poisons them wholesale with sprays, dusts, and gases, the effects of which are not limited to the pests for which they are intended. It is not surprising, therefore, that the complexities arising from these activities obscure the functioning of natural laws so that very simple reactions become incomprehensible.

An adequate understanding of the laws regulating insect populations seems to be an economic necessity. This is especially true of insects that attack low-value products like forest trees, or those that attack inaccessible parts of plants where they cannot easily be reached by chemicals. Such insects must be controlled by indirect means, that is, by the manipulation of the biotic or nutritional environment so that conditions become relatively unfavor-

able for the pests and thus bring the insect populations into equilibrium at a level favorable to man's interests.

The principles involved are probably common to all environments, but can best be studied in those places where man's influence is least felt. The forest provides an especially favorable ground for such population studies. In contrast to agricultural lands, where plowing, sowing, cultivating, spraying, and harvesting each follows on the heels of the other, year after year, forest lands may lie for many years undisturbed. Even in the most intensively managed forests, silvicultural procedures are separated by five- or ten-year periods, and in the extensively managed forests operations may be limited to occasional logging separated by several decades or even centuries. Thus of all the lands under man's control the forests are the least disturbed and the operation of natural laws are least obscured.

Unfortunately, the opportunities for population studies that the forest affords have only been slightly utilized. Forest entomology, like other economic aspects of entomology, has been continually pressed for immediately applicable results. Forest entomologists have been rushed from outbreak to outbreak where the pressure of circumstances has directed them, often arriving after the forest has been killed and the insects have departed, leaving desolation in their wake. Seldom, if ever, has a forest entomologist been on hand to observe the initial stage of an insect outbreak, and seldom has he taken time from his efforts at control to observe in detail the causes that bring about the decline of an outbreak.

Not infrequently, after organizing plans for control or even research, the outbreak suddenly collapses, leaving the entomologist in the midst of his preparations without any clear idea of what has happened. Under such circumstances parasites usually get the credit for checking the outbreaks, whether or not they have actually contributed much toward this end.

The purpose of this paper is twofold. First to present and comment on some of the few facts that we have observed concerning forest insect populations, and second to suggest investigations that should be instituted in the forest in order to throw light on the laws governing populations.

Insect populations in a forest normally exist under a condition of biotic balance. Hundreds of potentially injurious species occur generation after generation in moderate, economically insignificant numbers, each generation on the average giving rise to equal numbers in the following generation. Most of these species are not sufficiently numerous to be best subjects for population studies. A smaller number of species attain economically important numbers, and it is only these that we know enough about to discuss. From these we may hope to learn the causes of outbreaks and how populations may be kept in equilibrium. In this paper we shall confine our attentions to this economically injurious group that includes less than one per cent of all forest insects.

These insects may be divided for convenience into three groups characterized by three different population types, namely: (1) balanced populations at high density, (2) sporadically eruptive populations, and (3) periodically eruptive populations. Each of these will be discussed in order.

BALANCED POPULATIONS AT HIGH DENSITY

Balanced populations at high density are relatively rare in the forest. They usually occur under forest conditions that are abnormal and they injure trees without killing them outright.

One good illustration of this kind of insect is the white pine weevil, *Pissodes strobi*. This insect has become excessively abundant on second-growth eastern white pine, in the large seedling and small sapling stages. By killing the leading shoots year after year the excurrent habit of growth and the utility of the tree may be destroyed, but the tree will continue to live on indefinitely. Under the favorable conditions existing in pure stands of young pine, the weevil reaches equilibrium at a high level (MacAloney, 1930). This level is apparently determined by the size of the leading shoots both in length and diameter, the density of the stand, and by the activities of parasites and predators. In certain dense stands the level at equilibrium is often low; in open stands it is usually high. When pine is mixed with hardwoods the infestation falls to a point of economic insignificance (Graham, 1926).

Parasites doubtless play an important part in maintaining weevil equilibrium (Taylor, 1929 and 1930), but even more important is the diameter of the infested leaders. The flow of resin in the injured shoot forces the attacking larvae to advance down the stem side by side in a ring formation. Thus the circumference of the stem determines the number of progeny that may be produced by a single female, since a female usually lays her full quota of eggs on a single leader.

Another insect that often attains equilibrium at high density is the Nantucket pine moth, *Rhyaciana frustrana*. This also is a pest of young pines which destroys the tips, causing undesirable abnormalities of growth. Available evidence indicates that this insect is held at equilibrium by the action of parasites. In the absence of efficient parasites, it may run rampant for years as it did on the Nebraska National Forest and as it is now doing in forest plantations in Illinois, Indiana, and Kentucky. In most of its range, however, parasites hold it within economic limits except for occasional eruptions that are not understood.

Other insects that belong to this class are the European pine shoot-moth, *Rhyacionia buoliana;* the pitch-blister moths of pine, *Petrova* spp.; cone beetles, *Conophthorus* spp.; the cone moths, *Dioryctria* spp.; the locust borer, *Cyllene robiniae;* and various other insects that may be numerous without killing the trees on which they feed. Such insects as these appear to offer some of the best opportunities for the application of biotic control; in other instances, as in the case of the white pine weevil, silvicultural

procedures may be used to increase environmental resistance, thus reducing the population level below economically allowable limits.

SPORADIC OUTBREAKS

Some insects appear in sporadic outbreaks after living for years at a relatively low and economically insignificant population level. These eruptions follow as a result of temporarily changed environmental conditions. The pine barkbeetle, *Ips pini,* and many secondary barkbeetles are good illustrations. Sporadic outbreaks of these insects frequently occur in pine stands that have been thinned, in trees about building sites where coniferous trees have been cut, or where green coniferous wood has been used in construction, along newly constructed roads through coniferous forests, and in blow-downs. These outbreaks promptly disappear and the population returns to normal with a return to usual environmental conditions.

It seems clear that the cause behind these sporadic conditions is the temporary lowering of environmental resistance, ofter the result of a temporarily abundant food supply, or in other instances because of the baiting effects of attractive materials that tend to concentrate normal populations at certain spots. From the economic viewpoint these outbreaks are relatively inconsequential except, perhaps, those that follow blow-downs and thinning operations.

PERIODIC OUTBREAKS

Periodically eruptive outbreaks provide the forest entomologist with his most important and difficult problems. These outbreaks often occur at intervals of several decades and frequently destroy vast quantities of timber. But none have thus far exceeded in destructiveness the 1910-1920 eruption of the spruce budworm, *Cacoecia fumiferana.* At that time this insect destroyed a volume of wood sufficient to supply all the pulp mills then operating for a period of 40 years. In terms of values destroyed the spruce budworm ranks as public enemy No. 1 of the insect world. It is doubtful if the present outbreaks of the European spruce sawfly, *Neodiprion polytomum,* serious though they are, will change this rating. The eruptions of the larch sawfly, *Pristiphora ericksonii;* the hemlock loopers, *Ellopia fiscellaria* and *E. somniaria;* the forest tent caterpillar, *Malacosoma disstria;* and numerous other defoliators are so familiar that nearly every entomologist has had personal contact with some of them.

Although our knowledge of eruptive species is inadequate and incomplete, it may nevertheless be profitable to review some things that we do know and some things that we suspect about these insects.

The character of periodic outbreaks caused by various forest insects is similar in many respects. (1) They are characterized by tremendously concentrated populations which usually cause serious injury to the trees. (2) The outbreaks usually appear suddenly and disappear with equal suddenness.

(3) They usually occur during periods when weather conditions are especially favorable for the insects. (4) They usually, but not always, occur at the same time or about the same time over extensive areas, sometimes involving certain forest types over the greater portion of the geographic range of the host tree. (5) In most instances repeated eruptions seem likely to occur at more or less regular intervals. (6) Eruptions are more common in temperate than in tropical forests. (7) They are most frequent in forests where a single tree species predominates, and (8) are usually most common and most severe in overmature stands or in forests that are approaching maturity. Time will not permit the discussion of each point but let us consider the significance of some of these similarities.

The tremendously dense populations characteristic of eruptions have frequently attracted popular as well as scientific interest and are so familiar that they need only be mentioned here. The appearance of spruce budworm moths when in flight during an epidemic has been compared to a snowstorm in the tree tops. The forest tent caterpillars, when moving over the ground as they do, in search for undefoliated trees, have been so numerous that their crushed bodies on railroad tracks have made it impossible to pull trains up even slight grades. More recently this insect is said to have interfered similarly with automobile traffic on cement highways in infested areas.

Walking sticks become so abundant that their eggs falling on the ground suggest the patter of raindrops. This is truly no exaggeration. It is not surprising that the trees attacked by such hordes of insects are usually injured seriously.

The degree of injury, however, varies greatly. A single complete defoliation will kill hemlock, spruce, or balsam fir. Thus eruptions of the hemlock looper spell the immediate destruction of the heavily attacked trees. The spruce budworms feeds mostly on the current year's foliage, leaving the older needles, with the result that it kills trees only after several seasons of defoliation. The jack pine sawfly, *Neodiprion banksianae*, and many other sawflies prefer old needles, and therefore do not kill trees by a single attack, but some like LeConte's sawfly, *Neodiprion lecontii*, may completely strip and kill trees in a single year.

Hardwoods and deciduous conifers are able to send out new leaves after defoliation and therefore can survive as many as three successive years of defoliation. Thus on these trees eruptions that are of short duration may only reduce growth temporarily and cause no mortality. Dendroctonus beetle eruptions, on the other hand, may cause the death of practically every tree attacked.

The sudden appearance of outbreaks is often cause for astonishment. The assumption is frequently made that the hordes of insects have flown in from some other locality. Invasions do occasionally occur, but it is not necessary to assume an invasion to explain the sudden appearance of an

outbreak. Take the spruce budworm for instance. This insect has a biotic potential of approximately 200 progeny per moth and an average increase of 100 young per moth has actually been observed in the field (Graham, 1935). Subsequent losses observed during the larval and pupal stages have been as low as 27 per cent of these stages. Under these conditions a 73-fold increase would be possible. Thus if the moth population per tree started at 50, an insignificant number that would not be noticed in terms of defoliation, in the second generation it would be 3,650, a moderate infestation, and in the following generation 266,450, a number that probably could not be supported by the foliage on an 8-inch tree. Thus the potentialities for increase are so great that in two or three seasons of low environmental resistance a population can grow from insignificant numbers to outbreak proportions in an apparently miraculous manner.

Although the rise of defoliator eruptions has seldom, if ever, been observed accurately in the field, their effects on tree growth make it possible to reconstruct, in part at least, the way in which some outbreaks have built up. What information is available indicates that individual trees are attacked first. Presumably these may be the most susceptible trees in the stand. Then after a year or two, when the population has built up sufficiently, the entire forest will be attacked.

Sometimes it appears that groups of trees may be attacked first and that these foci of infestation will spread rapidly and coalesce. Usually there seems to be a movement, generally with the prevailing wind, into adjacent uninfested territory. Thus the spruce budworm in northern Minnesota appeared first in 1912 and reached a peak in St. Louis County and parts of Lake County. In 1918 it appeared in adjacent areas to the east in Lake and Cook counties, and still later in 1923 appeared in abundance in eastern Cook County. These infestations seemed to be like successive waves from a concentrated population, the 1918 wave being less intense than the original infestation and the 1923 wave being still less intense. The spacing of these dates might suggest a cyclic behavior for the budworm comparable with grouse and hare cycles, but without more information this similarity should not be taken seriously.

Although population eruptions are usually sudden, there are some instances in which they develop slowly. For instance, the walking sticks in parts of Michigan (Graham, 1937) become established in favorable spots where they increase tremendously in numbers. From these centers they spread out into adjacent favorable timber at a maximum rate of one-eighth mile per year and a minimum observed rate of one twenty-fifth mile per year. Because these insects do not defoliate the trees until late in the summer after the season's growth is almost complete, the injured trees do not succumb until after ten to fifteen years of defoliation. Ultimately the outbreak dies out with the death of the favored food trees. Thus the walking stick outbreak is character-

ized by a slow increase and spread followed by a correspondingly slow decline associated with the death of the host trees.

There seems to be a very clear correlation between weather and insect outbreaks. This relation has been almost universally observed, and as a result a strong feeling has developed that insect outbreaks are the direct result of weather fluctuations. Keen (1937), Craighead (1925), Miller (1933), and other workers have shown definite correlation between Dendroctonus outbreaks and weather. Spruce budworm outbreaks on pine are usually associated with drought. Likewise in Europe dry weather is often associated with outbreaks of the nun moth and other defoliators (Knoche, 1929). Scale insect outbreaks are most frequent during dry periods and adelgids are least abundant when heavy rains occur in the spring and early summer (Wilford, 1937).

In certain instances the ways in which weather affects forest insect populations have been studied with some degree of success. The production on pine of staminate flowers is most prolific during dry periods and therefore the presence of this especially favored food of the young spruce budworm larvae results in rapid growth of the population. Adelgids are likely to be washed away and destroyed by heavy rains during the flight and hatching periods. Drought reduces the vitality of trees so that they offer conditions for barkbeetle multiplication that are more favorable than in normal years.

On the other hand, adverse weather conditions may temporarily reduce insect populations, but usually these effects are short-lived when conditions return to normal. For instance, very cold weather may destroy barkbeetle broods, but seldom brings outbreaks under control because after such decimations the insects breed up rapidly (Keen and Furniss, 1937). Although it is dangerous to generalize from limited evidence, it appears that on the whole the effects of favorable weather influence insect populations more than do the unfavorable variations. They often constitute the spark to touch off conflagrations, the fuel for which has been prepared and is waiting for favorable conditions. Unfavorable weather is not uniformly severe over any area. Otherwise extermination of the insects would result. On the other hand certain spots of variable size remain favorable and thus weather extremes force the insects back into these niches that remain favorable, and from these spots they may emerge and multiply rapidly when general conditions improve.

Although outbreaks are often associated with favorable weather, it is nevertheless evident that infestations of forest insects are not of uniform intensity throughout the forests involved, even though desirable food plants may appear to be generally distributed. For instance, the hemlock looper reaches its highest population concentration only in pure stands of hemlock and is seldom seriously injurious in forests that are composed of less than 50 per cent of this tree. Also the forest tent caterpillar becomes eruptive

only in pure or nearly pure stands of aspen, oak, or maple. In this instance, as in the case of the spruce budworm, it seems likely that biotic races that are especially adapted to one of these tree species explains the fact that any one outbreak is ordinarily limited to a single tree species.

There are many similar illustrations of the influence that forest composition exerts on insect populations, but those mentioned will serve to show that the abundance and distribution of the food trees play an important part in determining insect populations in the forest. From the viewpoint of control this dependence of insect populations upon the quantity, quality, and arrangement of food plants has considerable significance. If outbreaks were made possible only by the occurrence of favorable weather the hope of preventing such catastrophes would be slight except by expensive, direct procedures. If, however, the abundance of noxious insects may be limited by forest composition, then we are in a position to prevent many insect cataclysms by appropriate silvicultural treatments.

The cause of periodic eruptions of forest insects is frequently ascribed to the absence of predators and parasites. Likewise, the sudden decline of outbreaks is often said to be caused by these animals. It seems doubtful that an absence of predators or parasites has ever been demonstrated to have resulted in an outbreak of any native forest insect. It seems possible and even probable that outbreaks from this cause do occur, but it does seem that statements have been made and accepted that assume too much.

Likewise the sudden end of outbreaks are too frequently ascribed without adequate evidence to the action of these beneficial agencies. A high degree of parasitism at the end of an outbreak may be the result of host reduction from starvation or other causes rather than the cause of the reduction.

As an illustration of this, the observations of Tothill (1923) in connection with the great spruce budworm outbreak in New Brunswick may be cited. A sharp reduction in the budworm population followed the destruction of almost half the larvae by starvation and 11 per cent by storms. This was followed by a tremendous increase in the proportion of budworms destroyed by parasites and predators. Thus if only the final stage of the outbreak had been observed, the conclusion might easily have been drawn that biotic factors were the primary cause that brought the outbreak to an end. Under similar circumstances in Michigan we have observed partial starvation of the budworm to be followed by an astonishing change in sex ratio of emerging moths from approximately equal sexes to an unbalanced ratio of 25 males to one female, a change that in itself could bring about the end of an outbreak. Also under such conditions of unbalanced sex ratio the fecundity of the individual females was greatly reduced.

In contrast to the situation which he described in New Brunswick, Tothill (1922) records the end of a budworm outbreak in British Columbia that was definitely brought about by parasites and predators before serious

damage was caused. In this instance the budworm population was somewhat limited by relatively unfavorable forest composition, and birds destroyed 38 per cent and parasites 60 per cent of the budworms. Another similar instance was observed in northern Minnesota in 1924 when the Blackburnian warbler and other small birds were especially valuable in destroying the spruce budworm. The value of birds in controlling insects is commonly accepted. Only occasionally does someone (Strickland, 1928) point out the limitations of these animals in checking insect outbreaks. What evidence is available indicates that birds are efficient when the insects occur in moderate populations and therefore may play an important part in preventing eruptions. On the other hand they are helpless to check an outbreak once the eruption has gathered sufficient momentum and reached a density at which the insect food produced exceeds the amount required to satisfy the nutritional requirements of the bird populations. This is especially well illustrated by the information presented by Tothill (1922) from his study of the fall webworm, *Hyphantria cunea*. The following table is adapted from his data:

Efficiency of birds on fall webworm populations at various densities.

Year	1912	1913	1914	1915	1916	1917	1918
No. of webs along 80 miles of road	100	20	3	2	2	5	30
Per cent eaten by birds	9	53	87	88	90	74	73

From this table it will be seen that the proportion of the insects eaten by birds exhibits an inverse relationship to the abundance of the webworm.

In the preceding pages we have discussed some of the features that appear to characterize forest insect populations. Most of this information is incomplete and, although suggestive, is inadequate to provide even an approximately complete picture of conditions. It seems essential that much more information concerning population phenomena must be collected if forest insect populations are to be understood and regulated intelligently.

First of all, we must measure and express quantitatively the effects of the various factors of environmental resistance. In order to do this we must have some constant for the various insects in terms of which these factors can be expressed. The biotic potential[1] of the species answers this requirement. The resistance exerted by environmental factors can then be expressed in terms of reduction of potential numbers caused by each factor. In this way resistance factors may be reduced to common terms and expressed on a comparable numerical basis.

All this requires detailed field observations carefully planned on a long-time basis. It requires the establishment of permanent field laboratories and

[1] The capacity of an organism to reproduce in a given time in the absence of environmental resistance.

many observation points at which the important insect species may be observed quantitatively and qualitatively from season to season and from year to year. This will entail much detailed routine work and, although no great expense would necessarily be involved, regular and sustained financial support would be necessary.

It seems evident that the forest offers one of the best opportunities for studying insect populations, but what agency is to do this basic sort of research? This is a difficult question to answer. In more than one instance studies of this sort were started or were about to be instituted by public agencies such as the Bureau of Entomology and Plant Quarantine, the Entomological Branch of Canada, and various educational institutions. But changes in personnel, pressure from apparently important emergencies, and shifts in undependable appropriations left them unsupported. At present little is being done in this important field by any agency, but it is high time that some sustained support be found for long-time quantitative investigations concerned with insect populations.

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INSECT POPULATIONS IN RELATION TO BIOLOGICAL CONTROL

By

HARRY S. SMITH

University of California Citrus Experiment Station
Riverside, California

A really comprehensive discussion of the relations existing between biological control and populations of insects is obviously impossible in the time allotted since the whole subject of biological control falls within the scope of this title. For this reason only certain special features of this relation will be considered.

In this discussion the word *control* will be used to indicate the maintenance of a population density below the point where economic injury to man's interests occurs and "biological control" will be limited to such control by parasitic, predatory and pathogenic organisms. The expressions *balance, equilibrium,* or *steady state* will be used to refer to a condition where the rate of change of population density is zero or approximately so on the average, a condition which is of course independent of the absolute density.

Paradoxically, animal populations are characterized both by their stability and by their incessant change. Some biologists emphasize one of these aspects, some the other. Actually these expressions are both descriptive of animal populations just as much as they are descriptive of the weather, which changes from day to day but which over a longer period of time is very stable. These characterizations of populations are not inconsistent if it is remembered that they are meant in the relative sense only.

Population densities therefore have both static and dynamic qualities, the distinction being analogous to that between climate and weather. In considering the effect of biological or any other control agencies the two must always be carefully distinguished, because the same type of environmental factor may affect one characteristic of populations quite differently from the way it affects the other. This discussion is primarily concerned with the effect of biological control agencies on the populations of their hosts, and while in nature these biotic agencies can never be independent of such physical factors as climate, nevertheless climate influences primarily the degree of their effect, rather than the kind of effect. For this reason there is justification for considering the relation between population densities and biological control agencies independently of the rest of the environment.

Several specific characteristics of biological control agencies are important in this relation. For reasons of brevity only insect parasites and predators are considered, since they will serve to illustrate the underlying principles,

and only three characteristics are dealt with, namely, potential reproductive capacity (biotic potential); the "effective" rate of reproduction; and the power of discovery of the entomophagous insect.

The significance of potential reproductive capacity, used here to denote the maximum possible capacity to increase under conditions optimum for reproduction, is I believe often misunderstood. There is no positive correlation between the maximum possible rate of reproduction of a species and its average population density. It scarcely needs to be pointed out that the most abundant species are not necessarily the ones which can increase most rapidly, or that the rare species are not necessarily those having a very low reproductive capacity. Darwin devoted most of one chapter of his "Origin of Species" to a discussion of this question.

It seems evident that the potential reproductive capacity of a parasite is of practically no importance in determining its effect on the average population level of its host since, in a stable association, there will mature only one parasite per parent. Actually a parasite must oviposit in more than one host since there is some parasite mortality caused by eggs being deposited in host individuals that die for other reasons before producing parasites, but certainly in the steady state the parasite's capacity to lay eggs is far in excess of what is needed to enable it to control its host, and its effect on the host population is not therefore likely to be limited by its potential reproductive capacity.

We cannot, however, disregard its *effective* rate of increase under all conditions, for such influence as an entomophagous insect has on the rate of change of the population density of its host is determined by the difference between its effective rate of increase and that of its host.

In general then it may be said that the *potential* reproductive capacity of a parasite or predator, by itself, is of little or no importance in its relation to the population density of its host; that the *effective* rate of reproduction of a parasite or predator is important in its relation to the intensity of change in oscillations and outbreaks; and that in the steady state, since the mean rate of change of the host population is zero, the mean rate of change of the parasite's population also must be zero, and that this is true regardless of the population level. The per cent of hosts destroyed in the steady state by a parasite does not therefore give any indication of its effect on the average level of the host population.

By far the most important property of an entomophagous insect in relation to its effect on the population density of its host is its searching ability. Its capacity to discover hosts in relation to host density more than any other quality determines its effectiveness as a control agency. If a parasite species is to bring about equilibrium in the population of its host, that is, is to be the environmental factor which ultimately causes natality and mortality of the host to reach equality, it must be able to find (and to destroy, of course)

that fraction of the progeny of each host female which is surplus. That is to say progeny which, unless destroyed, would result in an *increase* in the population of the host. It must be able to produce mortality such that, when added to the mortality caused by all other environmental factors, the total equals the number of new host individuals produced. When this occurs, equilibrium has been attained. But note that this could occur at *any density*. From the biological control standpoint we are concerned primarily with the *absolute population density* at which this equilibrium is reached. What determines this? The answer is of fundamental importance and is found to be the searching ability of the parasite species or its capacity for discovery of the host in relation to the population density of the latter.

Let us consider a phytophagous insect which has been introduced from a foreign country and which has reached a condition of equilibrium or steady density that is at a level so high that it is economically injurious. The environment is already destroying as many individuals as are produced and perhaps a native parasite is the key agency. But in order to bring the pest *under control* by the biological method, another parasite (or a group of entomophagous species) must be introduced which will cause the environment to destroy as many individuals as are produced *at a lower population level*, or, in other words, when the host individuals are more widely separated. This requires that the newly introduced parasites find the surplus progeny when they are farther apart than the native parasite was able to find them. It is evident then that the relation between the destruction of the surplus progeny and their distance apart is what determines the effect of a biological control factor on the population density of the host, in so far as we are concerned with the magnitude of the steady density. A parasite therefore in order to be effective must have the ability to find and destroy the surplus progeny of its host at a low host density, whereas an ineffective parasite can accomplish the same thing, but only at a high density, even though each species of parasite destroys exactly the same percentage of hosts.[1] For this reason the searching ability of the parasite becomes a matter of prime importance, far outranking its reproductive capacity, since the latter is usually, if not always, more than ample.

The searching ability of a parasite is a composite of several qualities, both physical and psychological, important among which are (1) its power of locomotion; (2) its power of perception (of its host); (3) its power of survival; and (4) its aggressiveness and persistence. It is to these qualities that we must look for a measure of a parasite's effectiveness, rather than to its potential reproductive capacity.

The success of an entomophagous insect as a control factor is not, however, determined exclusively by its own qualities. A very important influence is the nature of the distribution of the host insect or prey. The

[1] The percentage of parasitization does not therefore measure the relative effectiveness of two parasites.

population density of an insect may be represented by a given average, but actually this average tells us nothing about the nature of its distribution or dispersion within the area occupied. It may be concentrated in groups or colonies within which the density is much higher than the average for the whole area. So that from the standpoint of biological control, in many cases at least, the type of host dispersion has a very important bearing on the effectiveness of a particular species of entomophagous insect. At a given *average* density, and providing the entomophagous insect originates within the area of heavy infestation, the actual distance which it must travel to find a succession of hosts is less where the individuals are closely grouped than where they are uniformly separated. For this reason, within certain limits the more the host dispersion tends toward the colonial type, the more effective an enemy of given powers of discovery is in maintaining its average density at a low value.

In measuring the capabilities of an entomophagous insect as a biological control factor one cannot then ignore the nature of the host's dispersion. A parasite's efficiency depends upon a combination of the two qualities, host dispersion and its own power of discovery.

Actual examples will serve to emphasize the importance of this point. Two species of coccinellids were introduced into California many years ago to control two species of scale insects. The first of these was the Vedalia, *Rhodolia cardinalis*, an enemy of the cottony cushion scale. The second was *Rhizobius ventralis*, attacking the black scale. The Vedalia as is well known was a great success. Rhizobius failed to live up to early expectations and is of little practical importance in the control of its host. So far as can be determined there is little difference in the intrinsic qualities of the adults of the two coccinellids. Their fecundity is approximately equal; they are both free from parasites; and there seems to be no appreciable difference in their ruggedness, longevity or in their searching ability. The larva of Vedalia however feeds within the large egg-sac of its host and there is sufficient food in a single egg-sac to bring a larva to maturity. The larva of Rhizobius, before it can become full grown must feed upon the young black scale which have left the parent scale and migrated some distance. The delicate young Rhizobius larva is not able to travel any great distance without food and consequently succumbs when the population of its host is sparse; whereas in the case of Vedalia, no matter how sparse the population of the host, there is sufficient food within easy reach to enable the larva to mature. The dispersion of the cottony cushion scale represents an extreme case of the colonial or group type. The real reason for the remarkable success of Vedalia is thus found primarily in the nature of the host's spatial distribution rather than in the intrinsic qualities of Vedalia itself, as is so often stated!

An important general conclusion that seems to be justified from consider-

ation of this question is that, other things being equal, host insects having the colonial type of distribution can be controlled by entomophagous insects which rank relatively low in their power of host-discovery, whereas hosts whose population tends toward uniform scattering can be controlled only by factors having a high power of host-discovery. This would usually mean insect parasites rather than insect predators, for most parasites fly in the host-seeking stage whereas, while adult predators fly, these insects are handicapped by the fact that they must *also* seek hosts in the wingless *larval* stage which has relatively low powers of locomotion.

This handicap is an important one and greatly limits the value of many insect predators as biological control agencies. Since a predatory larva *must* find a *succession* of hosts in order to reach maturity, and since its relatively weak powers of locomotion make this possible only at a fairly high host density or where the host distribution is of the colonial type, predatory insects *in general* cannot be considered to offer as much promise as parasites for biological control purposes. Curiously even though insect predators usually destroy *more* hosts per individual than do parasites, the low power of locomotion of their larvae makes them *less* efficient as control factors. There are of course important exceptions to this rule.

Since the nature of the spatial distribution of the individuals of an insect species thus has such an important bearing on its biological control, it would seem to be worth while to consider the influences which bear on this characteristic of population densities.

There are of course almost innumerable reasons for insects assuming a grouped or colonial distribution. Often it is due to a discontinuous distribution of the host plant itself. Sometimes it is correlated wth the host relations of the phytophagous insect, which may attack only special parts of the plant, such as for example scale insects on fruit. This effect is obvious and is simply the result of the nature of the host relations. But is such grouping limited to situations where the distribution of the host is noticeably discontinuous? We are all familiar with cases where this is not true. Even where the host species occurs continuously, there is often a striking grouping of some insect species which feeds upon it although so far as can be seen, the plants which support a dense population do not differ from those on which the insect is rare. There is no doubt but that there is sometimes a subtle difference in habitats or niches which could explain this effect, but often it is not the same plants, or the same areas which, year after year, bear the heavier populations. Population densities seem sometimes to shift about in the same general region for no apparent reason. These observations suggest that there may be causes at work other than differences in the ecological niches.

As a possible explanation of some of these peculiarities, I have been extremely interested in some theortical work by Nicholson (1933) and by Nicholson and Bailey (1935).

It is well known that several mathematicians who have studied animal population problems [Lotka (1925), Volterra (1928), Bailey (1931)], conclude that population oscillations are inherent in the nature of the interactions of a specific parasite and its host, even in a perfectly constant environment, and when the interaction is continuous and the generations nonconcurrent.

There is no reason to question the soundness of this conclusion under the assumptions made, but it would be extremely difficult to verify it experimentally with biological material. In order to avoid the introduction of an additional factor, which was not included in the assumptions of the mathematicians and which would influence the result, the progeny of the parent organisms would have to be distributed at random at all times throughout the environment. Actually of course the diffusion of progeny from the site where they are produced is limited and, unless they were artificially redistributed, the tendency would be to develop colonies independently of the effect of the interaction of host and parasite. This in itself would apparently cause oscillations to occur.

Whether or not oscillations would take place in a constant environment is however of merely academic interest in the present discussion. Under natural conditions an environment usually possesses fluctuating physical attributes, and this in itself tends to modify the seasonal history of insects in such a way as to produce something at least approaching distinct generations. I can see no objection therefore to the conclusion of Nicholson (1933) that if a specific parasite and host interact alone, and if the generations are maintained distinct so that the stages of the host are synchronized, oscillations would follow as shown in the graph (Fig. 1). The intensity of the resistance to population growth exerted by the parasites against any particular generation of hosts is regulated by the population density of hosts of the previous generation, since it is the previous generation that determines the number of parasites. Nicholson and Bailey (1935) show that both the parasites and hosts oscillate perpetually about their respective equilibrium positions, but because of this *lag* in the oscillation of the parasite in relation to that of the host, the oscillations tend continually to increase in amplitude. As the graph (Fig. 1) shows, when the host is at its steady density the parasites are periodically at either a maximum or minimum so that they are able to destroy more than or less than the surplus progeny of the host, causing its population either to increase or to diminish. Diminution of the host population causes the numbers of parasites to fall below their average, with the result that the host is partially freed from the destructive action of the parasites and therefore increases to a point well above its average density. This high density then produces more than the average number of parasites and so on, the force applied by the parasites being alternately greater than and less than necessary to maintain the steady density.

It is obvious of course, as the authors point out, that the amplitude of these oscillations can not actually increase indefinitely. The *tendency* for them to do this, however, produces a very interesting result. "Each female is the center of diffusion of her offspring, so when the density of a species becomes very low as a result of violent oscillation, the zones of diffusion from the various females can seldom overlap and may frequently be separated from one another by great intervals. Thus the interacting animals exist

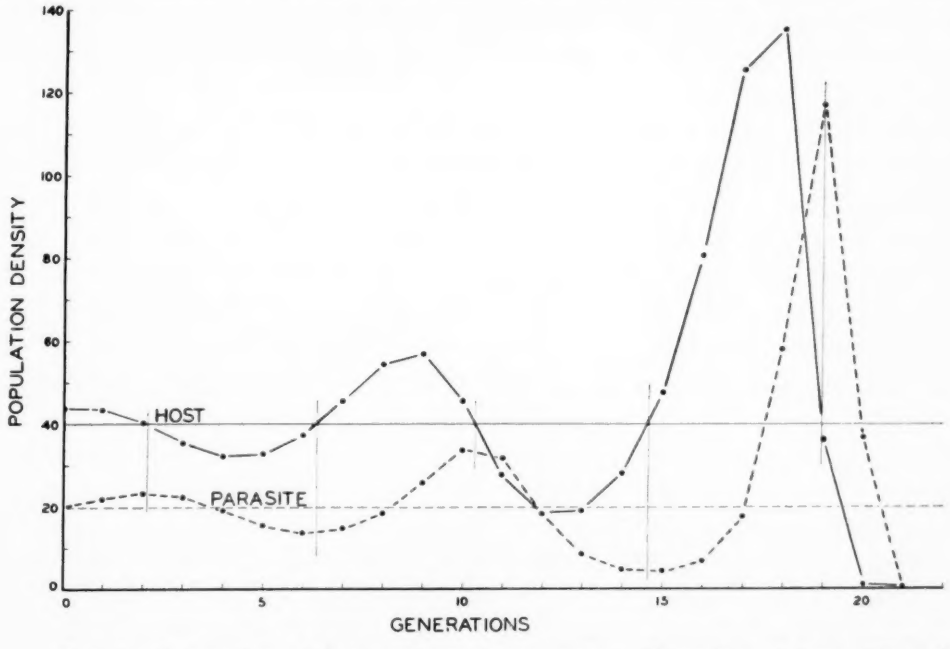

FIG. 1.—Interaction of host and specific parasite. Fecundity of host (F) = 2; power of discovery of parasite (a) 0.035. Original arbitrary displacement of initial host density from 40 to 44. Host curve shows initial host density, i.e., density of progeny at beginning of generation. Horizontal lines show steady densities of host (h) and parasite (p). Computed from formulae

$$h_{n+1} = Fh_n e^{-ap_n},$$

$$p_{n+1} = Fh_n - h_{n+1}$$

Note that when host population passes through steady density parasite density is either a maximum or a minimum.
(Adapted from Nicholson and Bailey, 1935).

in numerous disconnected small groups, within each of which interspecific oscillation follows its course independently of that in the other groups. Since the numbers of animals in these groups are very small compared with species-populations, the great reduction in numbers soon produced by increasing oscillation frequently exterminates the groups, but meanwhile some hosts will have migrated into the surrounding previously unoccupied country and will have established new groups there. . . . A probable ultimate effect of increasing oscillation is the breaking up of the species-population into numerous small widely separated groups, which wax and wane and then

disappear, to be replaced by new groups in previously unoccupied situations" (Nicholson and Bailey, 1935, pp. 389-390).

This interesting hypothesis of Nicholson's certainly provides a possible explanation of some of the peculiarly "spotted" distributions of population densities which we see in nature. Although only parasites were mentioned in this connection, the same condition could be brought about by almost any density-dependent control factor such as for example infectious diseases, in which there was a "lag" between the time the intensity of the resistance was determined by the host population and the time it was exerted *against* the host population.

Not only does the interaction between a host and specific parasite seem capable of producing a spotted distribution, but a spotted distribution in turn may increase the effectiveness of the parasite as a control factor, in so far as the average host density is concerned.

The distribution of these oscillating groups or colonies, in both time and space, and their population densities, would depend on the interrelations between the power of dispersion of the host, its effective rate of increase and the power of discovery of the parasite. Thus if a parasite having a low power of discovery interacts with a host having high powers of dispersal, extreme oscillation at a high average density will ensue. A parasite having high powers of discovery interacting with a host with low powers of dispersal will tend to produce slight oscillation at low average density, etc.

Many other interesting relations between population densities of insects and biological control agencies might be considered, such as for example the part played by specific as opposed to general parasites; the effect of parasites which compete for the same host; the effect of hyperparasitism and superparasitism; the effect of synchronization of host and parasite biologies, etc., but the time limit prevents.

The relations between population densities of insects and biological control which seem to be of paramount importance may be summarized as follows:

Population densities of insects have both static and dynamic aspects.

Since the direction and rates of population growth, as seen in cyclic changes such as oscillations and outbreaks, are determined by the relative birth and death rates, the per cent of parasitization may have an important influence on the rate of growth, but it does not determine the mean density from which this growth is measured. No matter what the mean density is, births and deaths are equal on the average and therefore the total per cent mortality is fixed by the birth rate. The effect of parasitism on the mean population density of a host species can be determined only by studying how the per cent of parasitization is influenced by changes in the population density of a host species.

Since in species which are in equilibrium with their environment only one of the young per parent can reach maturity, the potential reproductive

capacity of a parasite can not be a very important factor in determining its influence on the average population density of its host. Most parasites have a far greater reproductive capacity than is ever required under a condition of population equilibrium.

The power of discovery of a parasite determines the host population level at which it, together with the other environmental factors, is able to destroy the surplus progeny of its host and thus check further increase.

Insect predators as a group are less effective as control agencies than are parasites, since predators must seek hosts in the wingless larval stage, which has a low power of host discovery.

The nature of the host distribution is also of very great importance in determining the effectiveness of an entomophagous insect in the control of its host.

The interaction of a specific parasite and its host appears to be such that the population of the latter tends to be broken up into relatively small colonies which increase in density, reach a peak and then undergo near extermination while new colonies are building up in the vicinity. This hypothesis seems capable of accounting for some of the peculiarly "spotted" distributions of populations that are often seen in nature and which are not correlated with special ecological niches.

It is quite obvious that some of the foregoing ideas still remain to be verified. In fact, the main impression most of those who sit through this symposium will carry away is that we really *know* practically nothing regarding the principles underlying the regulation of population densities of insects in nature. No doubt this was in the minds of those who organized this symposium, and perhaps their principal purpose was to emphasize this fact in the hope that, as Professor Graham has so strongly urged, something really comprehensive might be done about it.

So far as the field investigations are concerned, forest insects are ideal subjects for such long-time research. They are of sufficient economic importance that the expenditure of considerable sums of money in their study could be justified from the practical standpoint and, most important, their responses are not continually upset by agricultural practices, as is true of most other economic groups. But the problems of animal populations are too complicated to permit solution by observation and deduction alone. None of the methods available to the scientist must be overlooked.

Although perhaps some biologists will not agree, I believe we are extremely fortunate that several of the leading mathematicians have interested themselves in the subject and have published extensively the results of their analyses. I may mention particularly the work of Lotka, Volterra, Bailey and Kostitzin.[2] The great advantage which population students may gain from these studies is that they suggest numerous hypotheses regarding the interactions of organisms which would never otherwise occur to even the most

[2] W. R. Thompson seems to have been the first to make *extensive* use of the method of mathematical analysis in the study of insect populations (Thompson, 1923).

imaginative mind. The experimental testing of these is certain greatly to advance our knowledge of the subject. In that admirable work by Nicholson and Bailey, "The Balance of Animal Population," will be found enough population problems to keep several laboratories busy for the next twenty years.

There are biologists who feel that in the study of animal populations theoretical studies are occupying the field to an excessive extent at this time. I for one have no fear of such a tendency so long as biologists do not forget that an hypothesis is only a means to an end.

There is no doubt, however, but that the time has now arrived when we as entomologists should give more serious attention to the experimental testing of population theory. It is true that the experimental study of insect populations has not been entirely neglected. Pearl and his associates made a start with Drosophila, Chapman has worked with Tribolium, to be followed by Holdaway, Stanley and Park, to mention only a few. Some most excellent work is being turned out by Salt, Laing and associates at Cambridge, and of course the experimental work done by Gause and others working with organisms other than insects is all fundamental to an understanding of this problem.

But when we consider that, basically, insects are economic problems only because of their numbers, is it not a just criticism that entomologists as a group have been somewhat slow to appreciate the need of and opportunities in population studies? There is here, it seems to me, a serious lack in our entomological program. It is a difficult situation to remedy, because it requires long time, expensive research. But an appreciation of the importance and complexity of the problem is the first essential. If this symposium shall bring that about, it will have been more than worth while.

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ECOLOGICAL RELATIONS OF CERTAIN ANIMALS IN DEAD PINE AND OAK LOGS

By

HARVEY EPPERSON SAVELY, JR.

Mississippa Delta State Teacher's College, Cleveland, Mississippi

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of Arts and Sciences of Duke University, Durham, North Carolina.

CONTENTS

PAGE

INTRODUCTION 323

LITERATURE 324

METHODS 327

Succession 327

Microclimate 328

Toleration of High Temperatures 329

Food Relations 330

RESULTS 332

Succession 332

In pines 333

In oaks 340

Microclimate 345

Toleration of High Temperatures 350

Food Relations 353

Tests for cellulase 356

Amounts Eaten 357

DISCUSSION 359

Succession 359

Microclimate 362

Toleration of High Temperatures 365

Nutrition of Wood Borers 367

General Discussion 370

SUMMARY 371

LITERATURE CITED 373

APPENDICES 377

I. Animals Collected from Pine Logs 377

II. Animals Collected from Oak Logs 381

ECOLOGICAL RELATIONS OF CERTAIN ANIMALS IN DEAD PINE AND OAK LOGS

INTRODUCTION

Many animals are known to live in dead tree trunks, and much is known of the habits of some of the species. Entomologists interested in economic species, taxonomists, and naturalists in general have long been interested in various groups. The purpose of this study was to make a general survey of animals in dead pine and oak tree trunks that had been cut for various lengths of time and to study the relations of certain species to their environment. A fallen tree trunk, which will be referred to as a log, is recognized as harboring a small, separate society that normally constitutes a unit (stratum) in a forest association. A log also has a microclimate that is different in many respects from climatic conditions in other parts of a forest (Graham, 1925). The knowledge of this led to the study of the factors involved in the microclimate of logs and this in turn to the effects of high temperatures and various humidities on representative species. In a study of a community of animals the subject of food is of great importance. It has been possible to deal with only a very few of the problems involved in food relations of animals in logs and their many individual physiological adaptations to their food supply.

The Duke Forest, in the midst of which Duke University is located, afforded an abundance of logs in all stages of decay, particularly of pines and oaks. For this reason, these two types of trees were selected for study. Collections were made in the Duke Forest wherever logs were found over a period of eighteen months, from September 1936, through February, 1938. All animals except nematodes and protozoans were collected. It is believed that most of the common species in the Duke Forest were thus obtained, but the number of species found is far short of all those that probably occur in the logs studied.

I wish to express my gratitude to Dr. A. S. Pearse, who suggested this problem and has given many helpful suggestions and criticisms. I am indebted to the following people for the indicated identifications: Dr. H. B. Mills, Collembola; Dr. A. B. Gurney, Orthoptera and Zoraptera; Dr. H. G. Barber, Heteroptera; Dr. Z. P. Metcalf, Homoptera; Dr. L. L. Buchanan, Dr. W. S. Fisher, Dr. E. A. Chapin, Dr. H. S. Barber, Dr. M. W. Blackman, and Dr. C. S. Brimley, Coleoptera; Dr. R. A. St. George, Tenebrionidae (larvae); Dr. Carl Heinrich, Lepidoptera; Dr. David G. Hall, Dr. Alan Stone, and Dr. C. T. Greene, Diptera; Dr. Grace Sandhouse, Dr. C. F. W. Muesebeck, and Dr. R. A. Cushman, Hymenoptera; Dr. M. R. Smith and

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LITERATURE

SUCCESSION

The change in the fauna of logs from the time they are dead until they are completely decayed is obvious to anyone who has had much experience collecting from them, and is common knowledge to those who are familiar with forest insects. Systematic studies of logs with the view of obtaining more exact information about these changes have, however, been undertaken in only a few cases. Probably the development of the field of ecology is responsible for directing attention to logs as the habitat of a characteristic group of animals, where previously only individual species or a small number of species had been studied. Many of the early accounts of insects in rotting logs have been incidentally included in works dealing with economically important species, which are present only in weakened or recently dead trees (Packard 1890, Townsend 1886, Felt 1906). Most of the insects first attacking a tree after it dies are fairly well known since they are of economic importance.

Shelford (1913) recognized fallen tree trunks as constituting an ecological unit (stratum) in forest associations and pointed out that there is a succession of animals in a log as it decays. Stages in the succession in beech logs were outlined, and some of the characteristic animals named. Adams (1915) gave a more detailed account of the succession of species in decaying tree trunks. He pointed out that the first animals to enter a log feed in the phloem layer in which starches and sugars are stored. These species aid the entrance of wood-destroying and other fungi and after the phloem has been destroyed and the wood has begun to decay, species of animals that prefer rotten wood make their entrance. As a log sinks lower and lower into the soil and becomes covered with leaves, it blends with the humus of the forest floor. Thus, Adams says, is completed one of the most important cycles of transformation to be found in the forest habitat. Blackman and Stage (1918) bred insects from larch and list those associated with that tree the first year

after it dies. Graham (1925) studied the early invaders of coniferous logs in relation to the temperature and moisture content of the wood and discussed the factors influencing ecological succession in logs.

The work of Blackman and Stage (1924) demonstrated the succession of insects in dead hickory. Their results were obtained by caging samples of wood over a period of five years and taking the insects that emerged. Their views of succession were in accord with those of Shelford (1913) and Adams (1915). Species of animals occurring in pine stumps on a burned English heath were recorded by Richards (1926). He indicated their general food habits and the stage of decay in which they occurred (whether early or late).

MICROCLIMATE

During the past few years the term "microclimate" has come into general use in ecological literature. Uvarov (1931) points out that in ecological studies climate of the actual habitat in which an animal lives must be considered, because the standard climatic data often do not accurately represent the conditions to which an animal may be subjected. He proposes to call the climatic factors that obtain in a given medium, such as a tree trunk, a microclimate. A study of the microclimate of the actual medium where an animal lives becomes, therefore, inevitable if all the conditions to which it is subjected are to be understood.

The temperature in logs exposed to the sun has been found to vary widely from that in air. Craighead (1920) found that when logs were exposed to the sun in summer that temperatures under the bark might reach 60°C., resulting in the death of certain wood borers. This discovery led to further experiments on the application of this method for the control of injurious bark beetles (Patterson, 1930; Miller, 1931). Graham (1921, 1922, 1924, 1925) has found that the temperature under the bark of logs does not depend entirely on the air temperature but on several other factors, chief of which are: intensity of solar radiation; angle of incidence of the sun rays; color, thickness and structure of the bark; evaporation from the bark surface; air movement; and the relative humidity and temperature of surrounding air. Graham showed further that the larvae of wood borers differed in their distribution in a log according to the temperature gradient. Conspicuous for their toleration to high temperatures were species of Buprestidae and Scolytidae. The moisture gradient in a log was also shown to be correlated with the distribution of wood borers.

Harvey (1923a, 1923b) found that in winter the subcortical temperatures of plum trees with dark colored bark might be 4.5°C. warmer than similar trees with light colored bark. Gottlieb (1929) reports that pine logs about six inches in diameter have the highest subcortical temperature when exposed to the sun, other factors being equal. It has been shown that when rotten oak logs are covered with snow, temperatures in the logs did not go

below —1.5°C. even when air temperature reached —16°C. (Holmquist, 1931).

No references to the composition of the air under the bark of logs or in cavities made by insects have been found in the literature.

TOLERATION OF HIGH TEMPERATURES

The toleration by insects of high temperatures has been investigated by many authors. The literature on the subject has been reviewed by Uvarov (1931) who finds that, in general, insects can survive temperatures up to 50°C. He points out, however, that most of the data are not comparable since hardly any two investigators used the same experimental conditions.

The work of Mellanby (1932) has recently added much to the knowledge of the relation of insects to temperature and relative humidity. He has shown that the upper limit of toleration to temperature for small insects (larvae of *Tenebrio molitor* and flea larvae weighing less than 100 mg.) is independent of relative humidity or evaporation deficit when they are exposed for short times (one to two hours). Such insects are said to die as a result of heat rather than desiccation. Longer exposure of the same insects (twenty-four hours) results in the death of those in low humidities at lower temperatures than those in high humidities, showing that over longer periods of time death may result from desiccation or a combination of heat and desiccation. When larger larvae (*Tenebrio molitor,* weighing more than 100 mg.) were subjected to similar conditions it was found that they survived a higher temperature in dry air than in moist air. Mellanby explains that this results from the cooling effect of the evaporation of water from the bodies of larvae in dry air, enabling them to maintain a body temperature lower than that of their surroundings. That certain insects can maintain a lower body temperature than that of their surroundings by the evaporation of water from their bodies has been shown by various authors (Necheles 1924, Buxton 1924). Mellanby (1935), in a review of literature on evaporation of water from insects, concludes that in general large insects may be capable of surviving higher temperature in dry air than in moist as a result of the cooling effect produced by evaporating water.

FOOD RELATIONS

Exact knowledge of the food eaten by many common insects found in logs is very meager. Uvarov (1928) pointed out that this was true of insects in general, and that before insects could be accurately classified as to their food habits, more exact information must be obtained for a large number of species. A summary of the food habits of North American families of Coleoptera was given by Weiss (1922). In other papers, Weiss (1923, 1924) and Weiss and West (1920) have shown a large number of insects associated with various fungi. Many of these insects occur under the bark of logs. The food habits of certain predacious Staphylidae were studied by Mank

(1923). Baumberger (1919) showed that certain dipterous larvae and mites living under bark feed on the hyphae and spores of fungi. Dipterous larvae of the genus Miastor also feed on fungi (Harris, 1923). The predacious habits of certain histerid beetles which as a family are considered to be saprophagous, were demonstrated by Selous (1911) and Steele (1927). The family Elateridae, whose members are largely plant feeders also include several predacious species (Fisher 1907, Thomas 1931). By examining the gut contents of carabid beetles Forbes (1883) found that many of them were not wholly predacious, and warned against suppositions as to an insect's food from its structural adaptations.

It has long been an unsettled question as to how certain insects can live on wood, since it is composed largely of cellulose and is poor in nitrogen. Cleveland (1925) at first thought termites could live without nitrogen, but it is now known that they are similar to other animals in requiring this element (Cook and Scott, 1933). The way in which insects utilize cellulose has had various explanations. Certain coleopterous larvae have been shown to secrete enzymes that break down cellulose (Cambell 1929, Ripper 1930, Falck 1930, Mansour and Mansour-Bek, 1934a). Microorganisms living in the gut of certain insects have been generally thought to enable their host to live on cellulose (Uvarov, 1928). Some evidence shows that the hosts digest part of the microorganisms (Wideman 1930, Hungate 1938). The general occurrence of mycetones in wood-eating insects had led to the assumption that they are in some way connected with cellulose digestion. Mansour and Mansour-Bek (1934b), however, are strongly opposed to such an assumption.

Another group of insects apparently do not depend at all on cellulose in wood for their carbohydrates, but subsist on stored starches and sugars in wood. This is particularly true of certain cerambycids living in the phloem of freshly cut trees (Mansour and Mansour-Bek, 1934a) and of *Lyctus* power-post beetles living in the xylem (Wilson 1933, Parkins 1936).

METHODS

Succession

Collections were made from logs and from slash of trees that had been cut for logs. Animals were found by peeling off the bark or by cutting into the wood with a hand ax. Some were preserved in alcohol and others were brought to the laboratory alive in one-ounce, metal, ointment boxes. Attempts were made to rear all larvae found. The larvae were put in individual ointment boxes with some of the wood from which they had been taken. These boxes were kept in a closed wooden cabinet at room temperature, a few drops of water being added from time to time. Wood-eating larvae were successfully reared when the moisture conditions were properly maintained and when they were not attacked by fungi.

All pine logs from which collections were made were probably either short leaf pine (*Pinus echinata* Mill) or loblolly pine (*Pinus taeda* L.), since these are the common species of pines in the Duke Forest. The common oaks in the Duke Forest are white oak (*Quercus alba* L.), southern red oak (*Quercus borealis* Michx., *rubra* L.), northern red oak (*Quercus borealis* Michx., *maxima* (Marsh) Ashe), black oak (*Quercus velutina* Lam.), and post oak (*Quercus stellata* Wang). No attempt was made to separate species of animals according to the species of oak or pine in which they were found. Logs were considered as either pines or oaks. No difficulty was found in distinguishing very rotten pines and oaks.

The cutting dates of many logs were obtained from the foreman of the Duke Forest. Though this paper, the "age of logs," refers to the length of time since the tree was felled and not the age of the tree. Where cutting dates were not available the age of a log was estimated by comparison with logs of known age. Since cutting dates were not available for many logs over three years old they were all classed as later stages.

MICROCLIMATE

Temperature in logs. Records of the temperature under the bark and in the wood of logs were obtained with a three pen, Friez thermograph, of the vapor pressure type, taking a weekly record sheet. Three thermograph bulbs made it possible to obtain simultaneous records at three separate points. The thermograph bulbs were 18 cm. long and 0.6 cm. in diameter, and were attached to the recorder by a 3.0 meter flexible cable. A hole of the proper diameter to take a bulb was bored in the end of a log to a depth great enough for the sensitive part of the bulb to be at least 12 cm. from the outside. After the bulb was inserted, the space around the cable was packed with sawdust or asbestos paper. The recording part of the instrument was housed in a standard Weather Bureau shelter. In the same shelter a combined hydrograph and air temperature recorder, making weekly records, was kept. The accuracy of both instruments was checked frequently with a thermometer. Temperatures as recorded by the instruments never differed more than $\pm$ 0.3°C. from the reading of the thermometer. Part of this inaccuracy results from the coarseness of the line traced on the record sheet by the recording pen.

These instruments were put into operation in February, 1937. Pine and oak logs that had been freshly cut, and one-, two-, and three-year-old logs were hauled to one place. They were from 30 cm. to 60 cm. in diameter and about two meters long. They were arranged parallel to each other in two rows and the weather shelter containing the instruments was placed between the rows. In this way, any log could be reached by the cable of the temperature recorder. The situation chosen was on level ground on top of a hill, in shade, in a stand of oaks. Records were obtained of the temperature at different depths in the series of logs.

The instruments were moved in June, 1937, to an open situation where temperature records were obtained from logs in full sun. During the winter of 1937-1938, temperature was recorded in logs in full sun and in logs in an advanced stage of decay.

Moisture of Wood. Samples of wood were collected in the field and placed in soil sample cans with tight covers. The samples were weighed and dried to constant weight at 105°C. Moisture was calculated as percentage of the dry weight of the wood.

Air in Logs. A survey was made of some logs that had been dead from 2 to 4 years to see if unusual amounts of CO_2 could be found in the air under the bark. Some preliminary trials during November and December were made, but the methods of sampling permitted a certain amount of contamination of the air sample. A mercury reservoir was attached by a convenient length of rubber tubing to a glass tube 8 cm. in diameter and about 25 cm. in length. Constrictions were placed in the glass tube near the ends to facilitate sealing with a blow torch. A needle was attached to the sample tube. A small hole was drilled through the bark and the needle was inserted quickly and packed with plasticene. The mercury had previously been brought up to the end of the needle. Thus, when the reservoir was lowered, a sample of gas was drawn into the sampling tube. The air sample obtained was approximately 10 cc. in volume.

During June and July the possibility of contamination of the sample was greatly lessened by rigid emplacements of copper tubing under the bark of several selected logs. These tubes were packed with putty and painted with shellac until there were no leaks around them. They were kept closed by a section of thick rubber tubing closed with a pinch clamp. A "T" of glass tubing placed between the sample tube and the copper tubing made it possible to expel all air from the sampling apparatus before a sample was drawn in.

The samples were analyzed in a Henderson modification of the Haldane apparatus.

TOLERATION OF HIGH TEMPERATURES

To test the toleration of some coleopterous larvae to high temperatures of two hours duration, two methods were used. By the first, a Warburg apparatus with Barcroft monometers was used. In the second, an apparatus similar to that used by Mellanby (1932) was used. In both methods relative humidity was controlled by the use of proper concentrations of an aqueous solution of potassium hydroxide following the tables given by Buxton and Mellanby (1934) for the relation between the specific gravity of the hydroxide solution and the humidity of the air over it. The water bath was heated electrically and the temperature controlled to within $\pm$ 0.25°C.

In testing the toleration of coleopterous larvae by the first method the following procedure was carried out. Solutions of potassium hydroxide were

made up to the required specific gravity for each degree of relative humidity used. One cc. of potassium hydroxide solution was placed in each manometer cup—0.5 cc. in side arm and 0.5 cc. in the central cup. The cups were then attached to the manometers and placed in the water bath and left for 10 to 15 minutes to allow them to reach the temperature of the water bath. The manometers were then removed. A larva that had been weighed was placed in each cup, and returned as quickly as possible to the bath to prevent too much cooling. After two hours, the larvae were removed from the bath, weighed and placed in petri dishes with moistened paper. It was not always possible to tell immediately if the larvae were alive after subjection to high temperatures, since they were limp and immobile. After two to three hours, however, a larva that had not been killed would usually move when it was disturbed. The procedure was repeated using fresh larvae and different temperatures until the limit of toleration was reached.

The apparatus for the second method consisted principally of a one-pint glass Mason fruit jar with a screw cap. A wide-mouthed bottle, small enough to go in the mouth of the Mason jar, was cemented bottom side down on the inside of the screw cap. A larva to be tested was placed in the small jar, over the mouth of which a piece of cheese cloth was secured with a rubber band. When the jar cap was screwed on, the small bottle cemented to it was suspended upside down over the potassium hydroxide solution with the larva resting on the cheese cloth. The jars were placed in a water bath for temperature regulation.

FOOD RELATIONS

In order to gain a knowledge of the materials eaten by certain insects, microscopic examinations were made of the gut contents and feces by spreading them out on a slide in glycerine. Fungus hyphae and spores could be identified as such, but the species of fungi to which they belonged were not determined. Predacious species were found to contain mostly liquid and semi-solid material in their gut. Interspersed in this material were many oily droplets. When such material was found in insects of unknown feeding habits it was assumed that it was of animal origin. This criterion was used by Forbes (1883) in similar studies on predacious Carabidae, and seems to be valid. In some cases fragments of exoskeletons could be identified, but species of animals that served as food could not be determined.

The habits of a cerambycid (*Callidium antennatum* Newn.) and a buprestid (*Chrysobothria* sp.) living under the bark of pine logs made it possible to determine the approximate amount of wood they consumed as larvae. A larva of *Callidium antennatum* Newn. begins its burrow entirely within the inner layer of phloem, which is from 0.5 to 1.5 millimeters thick, but as it grows it makes its burrow deeper by gnawing into the sapwood. An examination of the frass in the burrows showed that the fecal pellets contain only phloem, the greater portion of the frass being sapwood that

had never been eaten. When the larva is mature (in the prepupal instar) it makes a burrow 3 to 9 cm. into the sapwood toward the heartwood, and somewhat concentric with the annual rings. It then turns sharply and bores 5 to 10 cm. lengthwise of the grain. The frass accumulated from this boring is cast out of the burrow and some is pushed out through holes that are bored in the bark. The larva then seals itself into the end of its burrow with a tightly packed wad of fine frass.

When the bark was carefully removed from logs containing larvae, it was possible, in some cases, to expose the tortuous burrow of one larva that was separate from any other burrow. The fine, tightly packed frass in all of the burrow except in the area around the hole into the sapwood was removed. A piece of paper was then placed over the burrow and pressed with the fingers so that an impression was formed in the paper by the rim of the burrow. This impression was then outlined with a pencil and its area determined in the laboratory with a planimeter. Such data were obtained from October to December, 1937, at which time most of the larvae were in the sapwood in their cells. In each case the larvae were dug out, weighed, and placed in an oven at 60°C. to determine the amount of water they contained.

Ten samples of living phloem from five freshly cut loblolly pines from 20 to 30 cm. in diameter were collected in November, 1937. The bark was carefully removed so as to get all the living phloem off with the cork layer. Measured areas of the living phloem were then removed and placed in separate containers. The dry weight of these samples was then used to arrive at the average dry weight of the phloem covering one square centimeter of surface. The area of a burrow was multiplied by the average dry weight of the phloem covering one square centimeter of surface to obtain the approximate amount of wood that a larva had consumed.

Since *Chrysobothris* sp. had habits similar to *Callidium antennatum*, the same procedure was carried out for it. During the time when collections were made some were still feeding, while others were in cells in the sapwood.

Some qualitative tests for an enzyme attacking cellulose were carried out following a method similar to that described by Mansour and Mansour-Bek (1934a). The gut of the larva to be tested was dissected out and the juice it contained drained into a depression slide. A series of these slides were prepared using the juice from one larva, or from two larvae in the case of smaller individuals, for each slide. The materials tested were sections of lettuce midrib, slices of white pine wood, and filter paper. To each slide were added a few drops of toluol to prevent bacterial action. The slides were covered and left at room temperature. Control slides were prepared with water and boiled juice, to which were added the materials to be tested. They were examined after 6, 12, and 24 hours for evidence of breakdown of the fibers in the case of filter paper, or the cell walls in the case of wood

and lettuce, by removing the section from the slide, washing with water, and staining with zinc-chlor-iodide solution. Evidence of breakdown of the cell walls was taken as a positive test.

Portions of the gut contents of each larva were studied microscopically to see if bacteria or protozoa could be found that might possibly be considered as symbiotic.

Samples of living phloem were obtained from three freshly fallen shortleaf pines *(Pinus echinata)* in November, 1937. The samples were from trees about 30 cm. in diameter and were taken about 1.3 meters from the base of the tree. The living phloem was obtained by scraping it from the bark and sapwood after the bark was peeled off. The samples were dried at 105°C. and ground in a ball mill. The part passing through a 100 mesh screen was taken for analysis.

The method described by Sullivan (1935) was used for the determination of the amount of starch in two-gram portions of the ground wood samples. In this method, starch is extracted from the wood by boiling the sample in a concentrated calcium chloride solution. The starch is precipitated with alcohol and caught on a filter, redissolved in water, precipitated with iodide and ammonium sulphate and caught again on a filter. The starch is hydrolyzed with hydrochloric acid, and glucose determined by the Hagerdorn-Jenson method. The amount of starch is calculated by multiplying the glucose by the conversion factor, 0.9. For qualitative tests for starch, a potassium iodide-iodine solution was used.

RESULTS

SUCCESSION

A complete list of the animals collected from pines and from oaks is given in the appendix. The age of the log, where each species was found, the stage in its life cycle occurring in logs, the relative frequency of its occurrence, and its food habits are given. Estimates of the frequency of occurrence of the various species is based on the number of logs from which they were collected and their relative abundance in a log. The estimates are, therefore, not very accurate, but, in the writer's opinion, are better than no estimate at all. If an animal was found in over 50 per cent of the logs examined, it is considered to be "common." The occurrence of an animal in small numbers and in less than half the logs is called "occasional" in the table. Animals found only once or a few times are considered to be "rare." Those animals that are considered to be "common" undoubtedly include most of those important in the ecology of logs in the Duke Forest. Many species are known to breed in logs, and the number of species reported in this paper might easily be doubled by long and careful collecting. All the logs examined were in upland forest. Logs in swamps and river bottoms might contain additional species.

The small number of parasitic Hymenoptera and Diptera shown is due to the fact that no special effort was made to rear parasites from various hosts and therefore does not indicate their relative importance. Caged samples of wood containing larvae would undoubtedly have yielded many more parasitic Hymenoptera and Diptera. A total of about 155 pine logs were examined over a period of 18 months from September, 1936, to February, 1938. Over 135 species of animals were found. During the same period about 125 oak logs were examined and a total of over 165 species of animals were collected.

SUCCESSION IN PINES

First-Year Pine

About fifty logs of various sizes and in various situations (both in shade and exposed to sun) were examined. Collections were made in all seasons of the year from logs less than one year old. About 95 species of animals were found. Since a few species in several groups, particularly Diptera and Acarina, were not determined, a more exact number cannot be given. According to their known or probable feeding habits, the animals collected may be grouped as follows: phloem-feeders, 22; sapwood feeders, 4; saprophytic or myctetophagous, 37; predacious, 29; parasitic, 9. The number of species was distributed in various groups as follows: Insecta, 76; Myriapoda, 4; Chelonethida, 3; Acarina, 8. The Insecta were represented by the following orders: Collembola, 6; Thysanura, 1; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 55; Hymenoptera, 7; Diptera, 9.

The first animals found in logs after they were cut were beetles feeding in the phloem. In this group of animals there were eight cerambycids, four buprestids, three curculionids, and seven scolytids. As a result of the activity of these insects the bark becomes loosened from the sapwood. From an ecological viewpoint, the cerambycids and scolytids are very important, since they are responsible for most of the destruction of the phloem.

Monochammus titillator and *Acanthocinus obsoletus* were the most common cerambycids found, but under certain conditions other species were predominant. For example, in pine logs up to 30 cm. in diameter that were in contact with the ground and were in dense shade, the cerambycid *Rhagium lineatum* was commonly found, and in some cases, to the exclusion of other phloem feeders. *Rhagium lineatum* was also associated with *Monochammus titillator* and *Acanthocinus nodosus* in logs exposed to sunlight, but in such cases they confined their activities to the lower parts of a log, away from regions of bark that might be exposed to direct sun rays. *Acanthocinus nodosus* was rarely found in logs, but was a characteristic species in stumps. *Asemum moestum* was found only rarely in logs, but was common in stumps and the lower parts of standing dead trees.

In some pine poles, up to 20 cm. in diameter, that had been split from large logs and piled in open racks exposed to partial sunlight, a cerambycid,

Callidium antennatum, and a buprestid, *Chrysobothris* sp., were the only phloem feeders found. In certain racks a difference in the fauna of poles at different heights from the ground could be seen. In poles next to the ground, away from direct sunlight, *Rhagium lineatum* was the characteristic phloem feeder. In some cases *Asemum moestum* was also present. In certain poles, which were partially or totally shaded and about 0.6 meters above the ground. *Monochammus titillator, Acanthocinus obsoletus,* and *Ips calligraphus* were characteristic. Poles on top of racks about one to two meters high had become quite dry from exposure to the sun and contained only larvae of *Callidium antennatum* and *Chrysobothris* sp.

In general, species of scolytids and curculionids were more abundant in logs during the spring and early summer. Most of the pine logs examined had been cut in winter. Therefore the beetles probably oviposited in the spring when the phloem was still fresh. The fact that they complete their life cycle within three to four months would thus partially explain their greater abundance during the spring and early summer. Logs that had been cut in July contained many scolytids, principally *Ips calligraphus* and *Dendroctonus valens,* as late as the following November.

From the viewpoint of the amount of phloem they destroy, the most important scolytids in logs in the Duke Forest appear to be *Ips calligraphus* and *Ips grandicollis;* the most important curculionids, *Pissodes nemorensis* and *Hylobius pales. Pachylobius picivorus* was found only once.

Following the loosening of the bark by the activity of various beetles feeding in the phloem, another group of animals, having quite different habits from the phloem-feeders, begin to appear under the bark. In such situations about 60 species of animals were collected, most of which were insects. The orders of insects represented were: Collembola, 6; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 29; and Diptera, 3. Classed according to their known or probable food habits, there were 37 species found feeding on fungi or decaying animal and vegetable matter and 23 species with predatory habits. Collembolans, mites and Diptera were by far the most numerous from the standpoint of number of individuals. From the standpoint of number of species, the Coleoptera were most numerous, being represented by 29 species.

Predacious species associated with the subcortical fauna were of two types; those that lived entirely under the bark in the larval or adult stage, or both, and species such as centipedes and ants that were found running over the outside of logs as well as under the bark. The latter do not confine their activities to logs, but may also be found in the litter of the forest floor. Certain beetles were found that are predacious in both the larval and adult stage, such as ostomids, clerids, histerids, and staphylinids. Other species, such as *Alaus myops,* are predacious in logs only in the larval stage. Predacious insects associated with the phloem feeders were *Alaus myops, Tem-*

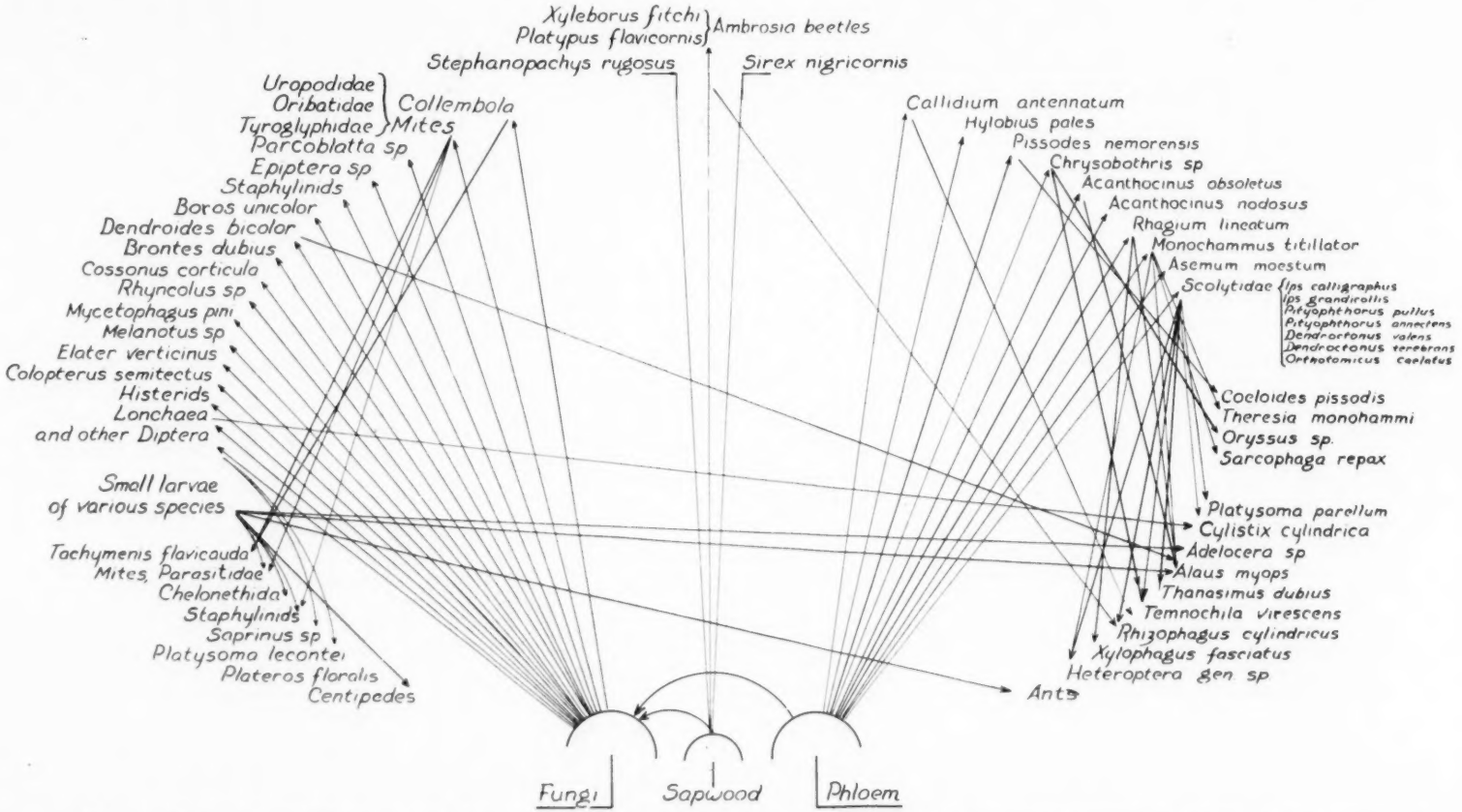


FIG. 1. The food relations of animals in a pine log the first summer after it is cut. The arrows point from the source of food to the animal consuming it. The figure is based on observations of logs in various situations and is not entirely applicable to any particular log.

nochila virescens, Thansimus dubius, and an unidentified heteropteran. The clerid, *Thanasimus dubius,* confines its attacks almost exclusively to scolytids. Adults prey on adult scolytids; larvae feed on the larval scolytids in their galleries under the bark. The unidentified heteropteran also feeds largely on scolytids both as a nymph and as an adult, but it was also seen to pierce the bodies of *Monochammus titillator* and *Acanthocinus nodosus. Temnochila virescens* and *Alaus myops* feed on various phloem feeders.

The parasitic Hymenoptera and Diptera collected were all from phloem-feeding larvae. Those obtained were usually reared from cocoons found in burrows.

Sapwood contained very few species of animals. A siricid, *Sirex nigricollis,* was the only species found that probably feeds for most of its life in the sapwood. Species of cerambycids and buprestids that form pupal chambers in the sapwood probably do not feed to any great extent on the wood removed from their burrows. Sapwood removed by *Monochammus titillator* in forming its pupal chamber is usually in long shreds which obviously have not been eaten. A platypodid, *Platypus flavicornis,* found in the sapwood, is known to be one of the ambrosia beetles that feed on fungi growing in its burrow. A scolytid, *Xyleborus fitchi,* also has similar habits. Species such as cerambycid, *Asemum moestum,* and the buprestids, *Buprestis* sp. and *Chalcophra* sp., apparently feed in the sapwood after they have first bored through the phloem, and continue to feed in it the second year after a tree is dead.

Second-Year Pine

About 50 logs, up to about 0.6 meters in diameter, exposed to various amounts of sunlight were examined. About 67 species of animals were found. Classed according to their known or probable food habits there were: phloem-feeders, none; sapwood-feeders, 11; saprophytic or mycetophagous, 28; predacious, 27; parasitic, none; nesting in log, 1. The number of species in each group of animals was as follows: Insecta, 54; Myriapods, 4; Chelonethida, 3; Acarina, 3; Mollusca, 2. The class Insecta was represented by six orders: Collembola, 6; Thysanura, 1; Orthoptera, 1; Isoptera, 1; Coleoptera, 36; Diptera, 4.

During the second year after a pine log is cut, the activity of wood-rotting fungi, which began during the first year, becomes more apparent. The two most common wood-rotting fungi in pine logs in the Duke Forest are *Polyporus abietinus* (Dicks) Fries and *Peniophora gigantea* (Fries) Massee. The bark is usually very loose and, after the emergence of the various phloem feeders, is punctured by many holes. This permits more water to get under the bark during rains, and at the same time probably permits more rapid evaporation of water from under the bark. In most of the logs investigated the phloem had been entirely eaten away during the first year. Small logs exposed to the sunlight or not in contact with the ground

were exceptions. They were probably much drier than larger logs which were either partially shaded or in contact with the ground.

The characteristic phloem-feeding insects of the first year logs are not present during the second year, except such species as *Asemum moestum*, *Buprestis* sp. and *Chalcophoro* sp. all of which were found in rotting sapwood. Eleven species of insects were found feeding in the sapwood. The most characteristic of these was the termite, *Reticulitermes flavipes*. It was rarely found in logs less than one year old, but during the second year, large colonies were frequent in logs in contact with the ground. Species of elaterids that entered logs the first year and fed on frass were also present, but in many cases they were feeding in sapwood that had become soft from wood-rotting fungi. Larvae of the tenebrionid, *Xylopinus rufipes*, and the melandryid, *Hypulus concolor*, were found feeding in soft rotting sapwood. A species of Bostrichidae, commonly called "powder-post beetles," was found in pine holes that had been piled in open racks exposed to sunlight.

The subcortical fauna of animals that followed the phloem-feeders into logs the first year was present during the second year. Larvae of *Dendroides bicolor* and *Boros unicolor*, both typical subcortical larvae, were more abundant. Nests of the ants, *Camponotus herculeanus pennsylvanica* and *Leptinothrox curvispinosus* were common. In some logs two or more large colonies were found.

Species of predators, such as *Thanasimus dubius*, *Temnochilla virescens*, and an unidentified heteropteran, that was associated with phloem-feeders in the first year were not found. *Alaus myops*, however, was present. Larvae of this species found in one-year-old logs had never been longer than 10 to 15 mm., but in two-year-old logs larvae up to 30 mm. in length were found. It seems probable that they require at least two years for their development. A pupa and an adult were found in October, 1937, in a large pine stump that was about two years old. Small larvae (up to 10 mm. long) of *Alaus myops* were also found, which indicates that the females do not restrict their oviposition to first-year logs. Predators, such as species of histerids and staphylinids, that probably feed on mycetophagous species were still present. Nests of a solitary wasp *Trypoxylon clavatum* were found in the emergence holes of *Monochammus titillator* and *Acanthocinus nodosus*.

Third-Year Pine

About 30 logs that were between two and three years old were examined. Logs of this age usually had little bark left on them, especially if it had been thin. Bark as thick as 3 cm. and over was usually still on a log during the third year, but such bark was found only on logs as much as 40 to 50 cm. in diameter. The extent to which logs had rotted varied. Logs in the forest, where they were partially shaded were attacked by fungi to a greater extent than logs exposed to more sunlight. In some places on a log fungi

often had reduced the sapwood to a punky condition, while on the same logs areas that had not been attacked to such an extent could be found. When bark had fallen away, the sapwood was relatively solid for a depth of 2 to 5 cm., forming a rather solid shell of wood around the log. Beneath this shell the sapwood was usually rotted to a much greater extent, and contained more moisture.

About 50 species of animals were collected. According to their known or probable food habits, they may be grouped as follows: feeding on rotting sapwood, 15; saprophytic or mycetophagous, 25; predacious, 12; nesting in logs, 1. Most of the insects found in two-year-old logs were also found in three-year-old logs, along with several additional species. Termites were still present with the addition of another large elaterid larvae, *Orthostethus infuscatus*. Two tenebrionids not previously found were *Uloma punctulata* and *Scotobates calcaratus*. Both species were characteristic of soft punky wood. Larvae and adults of *Uloma punctulata*, both of which feed on rotting wood, were present. *Xylopinus rufipes* larvae had been found in two-year-old logs and were still quite common in soft wood. Another species found for the first time was an Oedomerid, *Copidita thoracica*. A cerambycid larva belonging to the genus *Leptura* was also found in three-year-old logs, and is probably the same species found in two-year-old logs. *Passalus cornutus* were present in only one log.

The presence of a subcortical fauna was, of course, dependent on the presence of bark. The number of species was not as great as in the first- and second-year logs. Collembola were common and always associated with them was a carabid *Tachymenis flavicauda*. Larvae and adults of a cucujid, *Brontes dubius*, were found in some logs. Under fragments of bark remaining on logs next to the ground, the larvae of *Dendroides bicolor* occurred. The adult of the weevils, *Cossonus corticola* and *Rhyncolus* sp. were present, but never in the large number found in first- and second-year logs. The snails *Euconulus cherisinus* and *Zonitoides arboreus* were found under logs and under bark. A slug, *Philomycus carolinensis* was present under the bark of some logs that were very moist.

Fewer species of predacious insects were collected than in one- and two-year-old logs, chiefly because fewer predacious staphylinids and histerids were taken. *Alaus myops* was still present under bark and in the burrows of *Leptura* sp. and *Xylopinus rufipes*. Centipedes were common under bark, and in some cases small spiders were present, but the latter were not identified.

Logs Over Three Years Old

Since cutting dates for logs over three years old were not available, the latter stages of succession in pines could not be followed in logs of known age. In order to learn what animals might be present in the latter stages of decay, logs that were entirely softened or punky were selected for examination. Probably the age of logs over three or four years old is not very

significant because the amount of decay seems to vary considerably in logs of different sizes and under different conditions of moisture. The fungi that cause sapwood rot in pines in the Duke Forest usually leave the wood in a soft and somewhat stringy condition. Since the summer wood is attacked more slowly, the wood may be pulled apart with the hands into strips held together by summer wood. The bark had fallen off of most logs. Those exposed to partial sunlight usually had a dry shell of relatively sound wood from 3 to 6 cm. thick around them. Beneath this shell the wood had the typical punky texture.

Twenty-five logs were examined and over 35 species of animals were collected. The following groups of animals were represented by the number of species indicated: Insecta, 26; Acarina, 3 +; Myriapoda, 2; Mollusca, 2; Vertebrata, 1. The insects were represented by the following orders: Collembola, 4; Orthoptera, 1; Coleoptera, 14; Diptera, 3 ±; Hymenoptera, 3 ±. On the basis of their food habits, the animals collected may be classified as follows: feeding on rotting wood, 9; probably saprophytic or mycetophagous, 20; predacious, 7. A solitary bee, *Halictus* sp., was found in its nest in three logs. Larvae, pupae, and adults were collected in August, 1937. Species that were found for the first time were *Derobrachus brunneus*, *Halictus* sp., *Polygyra thyroidus*, *Polydesmus serratus*, and a salamander, *Plethodon glutinosus*.

The most common wood-feeders were elaterid larvae. Large larvae of *Orthostethus infuscata*, and smaller larvae of the genera *Melanotus* and *Elater* were common. *Derobrachus brunneus* was found in very rotten pine but there were never more than two or three individuals in a log. *Leptura* sp. was also present in moist wood. Probably the most characteristic insect of this stage of wood decay was a tenebrionid, *Uloma punctulata*, which feeds in both larval and adult stages on decayed wood. It was found in every log examined. *Reticulitermes flavipes* was present in a few rotten logs of this stage, but large colonies were never found. When present, it was attacking portions of log that were not punky. In a very moist wood, fly larvae belonging to the families Chironomidae, Cecidomyidae, and Dolicopodidae were found. Representatives of other families of flies probably occur in such wood. A snail, *Polygyra thyroidus* was present in three logs. *Philomycus carolinensis* was common in and under moist logs. Beneath logs the larvae of a lucanid, *Pseudolucanus capreolus*, were regularly found along with larvae of an unidentified scarabid.

A predacious carabid, *Tachmenis flavicauda*, was still present in moist wood where there were many collembolans. The larvae of *Alaus myops*, a predacious species, were collected in logs containing larvae of *Leptura* sp. and *Derobrachus brunneus*. A carabid, *Clivina* sp., was present in one log. This species is possibly not predacious, since other species of the genus are known to feed on sprouting corn (Blatchley, 1910). Adults of *Platysoma*

lecontei that were found were probably feeding on dipterous larvae with which they were associated. Only two species of centipedes were found, but it is likely that others occur since they migrate into logs from the soil.

None of the species found were very numerous in any log. In the logs examined there was a striking scarcity of animals in comparison to earlier stages of decay in pines, or in comparable stages of decay in oaks.

SUCCESSION IN OAKS

First-Year Oak

About 40 logs of various sizes and in various situations (both in shade and exposed to sun) were examined for animals. Collections were made in all seasons of the year from logs less than one year old, and about 50 species of animals were found. Unidentified species of Diptera and Acarina make it impossible to give a more exact number. The following groups were represented by the numbers of species indicated: Insecta, 37; Chilopoda, 2; Chelonethida, 2; Acarina, 9. Insects were represented by the following orders: Collembola, 4; Orthoptera, 1; Coleoptera, 2; Hymenoptera, 9; and Diptera, 3. All these animals may be classified according to their known or probable feeding habits as follows: feeding on phloem, 7; feeding in the sapwood, 1; saphrophytic, mycetophagous, or scavengers, 20; predacious, 17; parasitic, 5.

The common cerambycids found boring in phloem were *Xylotrechus colonus, Graphisurus fasciatus,* and *Romaleum atomarium. Neoclytus scutellaris* was found only once. Many other species are known to feed in the phloem of oak and doubtless occur in the Duke Forest, but are probably not of general occurrence.

Only one species of scolytid, *Orthotomicus collatus,* was collected. Most of the logs examined had been cut longer than six months, thus many scolytids had probably left the logs. The burrows of several species of scolytids could be seen in logs, but specimens were not obtained. Only one species was found feeding in the sapwood of oak logs less than a year old; this was a wood-boring hymenopteran, *Tremex columba.* In logs exposed to the sun only species of byprestids were found boring in the phloem on the top side of the logs. The most common species was *Chrysobothris femorata.* Larvae of a species of Dicerca were also present. Larvae of a species of Agrilus were very common in oak stumps, but only rarely present in oak logs. In the same logs in which buprestids were boring on the top side, larvae of *Romaleum atomarium* and *Graphisurus fasciatus* were consistently found boring in the phloem on the lower parts which were partially shaded, or did not receive the direct rays of the sun during the middle of the day.

The activity of phloem-feeding larvae had the effect of loosening the bark, but it also was found that the bark might become loosened by drying of the sapwood and bark. A subcortical fauna, not feeding on phloem, was

found where the bark had become loosened either by the action of phloem-feeding larvae or by drying of the sapwood. Some of the most characteristic species under such bark were Diptera. Larvae of a phorid, *Megaselia* sp. and a sapromyzid, *Lonchaea* sp., were bred. The larvae of *Lonchaea* sp. were often present in great numbers where the bark was moist. As many as 30 larvae were found in an area of about 25 cm.^{2} The phorids are probably predacious on other fly larvae. The cucujids, *Silvanus imbellis*, *S. planatus*, and *Brontes dubius* were in nearly every log that contained a subcortical fauna. Both adults and larvae were present. The adults, and probably the larvae, feed on fungi. Mites of several species were present in great numbers. Some, such as the Parasitidae, are doubtless predacious, while other species, such as the Uropodidae, probably feed on fungi, or are scavengers. Several species of Collembola were present. Other species feeding on fungi were staphylinids and a histerid, *Acritus exiguus*. The small histerids, *Bacanius punctiformis*, *Epierus* sp., and *Epierus regularis* also probably feed on fungi. The larvae of *Melanotus* sp. were common in frass left by wood-borers.

Probably the most characteristic predator in oak logs is a carabid, *Tachyta nana*. It feeds on mites and collembolans, and was present in every log examined that was sufficiently moist to be tolerable to its prey. The histerids, *Platysoma lecontei* and *P. carolinum*, were common under bark and were usually associated with fly larvae on which they feed. *Chariessa pilosa marginata* was common. It is predacious (Felt, 1906) and was associated with podurans, fly larvae, and cucujid larvae. All the parasite species were associated with wood-borers, and were usually reared from cocoons found in burrows. In some cases the remains of a cerambycid host made its identification possible. An unidentified tachinid was reared from *Romaleum atomarium* and larvae parasitized with as many as nine fly larvae (probably of the same species) were found.

Second-Year Oak

About 40 logs less than two years old were examined. A total of about 88 species of animals were collected, which belonged to the following groups: Insects, 68; Chilopoda, 6; Chelomethida, 2; Acarina, 9 +; Mollusca, 3. Insects were represented by the following orders: Collembola, 6; Thysanura, 1; Zoraptera, 1; Isoptera, 1; Orthoptera, 1; Coleoptera, 42; Hymenoptera, 9; Diptera, 4 ±. Classed according to their probable food habits, the animals may be divided thus: feeding in rotten sapwood, 19; feeding in phloem, 4; saprophytic and mycetophagous, 40 +; predacious, 30; parasitic, 4.

During the second year wood-rotting fungi, of which the polypores are most common, soften the sapwood, either generally or at least in scattered patches. The sapwood is usually not softened to a depth of more than 3 centimeters. The mycelia of fungi are often quite thick in the inner bark in logs that have not been entered by phloem-feeding insects. The bark is

always intact, but is punctured by the exit holes of buprestids, scolytids and cerambycids.

The phloem-feeding cerambycids *Romaleum atomarium* and *Graphisurus fasciatus* were still present. Larvae of a species of Dicera were found in some logs. Apparently the larvae of *Romaleum atomarium* require more than one year to complete their development. Two-year-old logs contained larvae which varied in size from mature to very small. This indicates that the females do not restrict their egg-laying to fresh logs. Larvae feed both on the inner bark and on rotten sapwood.

Several beetle larvae which bore in rotten wood were found for the first time. Apparently wood must first be attacked by fungi before these can enter. The most common species was the tenebrionid, *Alobates pennsylvanica.* It was observed that they were always burrowing in wood attacked by "white-rot" fungi. They were found in practically all logs examined. A related species *Merinus laevis* was found only once. The adults of *Passalus cornutus* were observed in newly formed burrows in rotten patches of wood. *Reticulitermes flavipes* were present in logs in contact with the ground, where they were tunneling through the rotten wood on the underside of logs. The burrows of the platypodid, *Platypus quadridentatus,* were often numerous in stumps and were present in most of the logs. They form tunnels in the sapwood and heartwood in which a fungus grows that serves as their food. A predacious colytid, *Colydium lineola,* was found in their burrows.

The tenebrionids, *Uloma punctulata, Xylopinus saperdoides, Dioedus punctatus,* and *Scotobates calcaratus,* were present in about half of the logs examined. They were never present in great numbers in logs less than two years old, but seemed to be more characteristic of more advanced stages of decay in which there was rotten sapwood.

The carpenter ant, *Camponotus herculeanus pennsylvanica,* was found in about 10 per cent of the logs examined. It excavates the sapwood and heartwood to form places for its nests.

The subcortical fauna was similar to that of logs during the latter part of the first year, but more species were collected. The melandryid, *Synchroa punctata,* and the pyrochorid, *Dendroides bicolor,* were found under bark in logs where the phloem had been eaten out by phloem-feeders. In the moist frass under the bark a great variety of species was found. Many such insects feed on fungi, while others are predacious. Collembolans and mites were numerous. A rare insect, *Zorotypus hubbardi,* was found under bark. Both nymphal stages and adults of an aradid bug, *Mezira granulata,* were common. The food of this insect was not determined. Essig (1926) says the aridid are predacious, and Comstock (1930) says they are supposed to feed on fungi. Nymphs of a fulgorid, *Epipera* sp., were found in small colonies feeding on a powdery looking fungus. Cockroaches were present under the bark of nearly every log.

Fly larvae of several species were present under the bark of every log that was moist. The number of individuals was often very great. They are probably an important source of food for many small predacious staphylinids, histerids, and other predacious species.

Typical predacious beetle larvae found were those of *Alaus oculatus, Chariessa pilosa cmariginata,* and certain staphylinids and histerids. Larvae of *Alaus oculatus* as long as 3 cm. were found, and, although there were never more than two or three in a log, their effect on the population of various larvae must be considerable. Adults of certain staphylinids and histerids were found that are doubtless predacious. Several specimens of Chelonethida (pseudoscorpions) were found under bark. Usually only one ore two were seen in a log. They are predacious, but, on account of their small size and their scarcity, cannot affect the community of animals in logs very much. Centipedes run through the litter on the forest floor and certain species are regularly found running over bark and into spaces under the bark. *Geophilus varians, Cryptops hyalina,* and *Linotaenia bidens* were common. They probably feed on various small larvae. *Geophilus varians* was once seen carrying a termite. *Scolopendra viridis* is a large species and was not as numerous as the small species. Usually only one or two were found in a log.

Third-Year Oak

Most logs between two and three years old no longer contain solid sapwood, but the heartwood is still solid. The bark is usually still intact. About 25 logs were examined, and the following groups of animals were represented by the numbers of species indicated: Insecta, 70; Chilopoda, 6; Diplopoda, 2; Chelonethida, 1; Acarina, 11 ±; Mollusca, 5; Annelida, 1. Insects were represented by the following orders: Collemolola, 3; Zoraptera, 1; Isoptera, 1; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 51; Hymenoptera, 6; Diptera, 4 ±; Lepidoptera, 1. The animals collected may be classified according to their known or probable food habits as follows: feeding on rotten sapwood, 20; feeding on fungi and rotten frass under bark, 50; predacious or scavengers, 25; on fungi in burrows in the heartwood, 1. The total number of species was 95.

About 25 species of animals were found in logs two to three years old that were not found in one- or two-year logs. Certain of these were charteristic of very rotten sapwood and heartwood. Such species were *Uloma punctulata, Dioedus punctatus, Scotobates calcaratus, Oylopinus saperdoides, Scolecocampa liburna,* and *Pseudolucanus capreolus.* Other species such as certain staphylinids, *Platypus quadridentatus, Eupsalis minuta, Euparius marmoreus, Chelanops* sp., *Tenebroides* sp., and certain oribatid mites possibly occur in younger logs, but they were not encountered.

The most characteristic wood-boring beetle larvae were those of *Alobates pennsylvanica. Passalus cornutus* occurred more frequently than in second-

year logs. *Romaleum atomarium* was still present, but only large larvae were found. Other species feeding on rotten wood were those that were previously mentioned as being new entrants into logs in the second year. *Reticulitermes flavipes* was a common inhabitant of rotting wood, and often occurred in large colonies, in contrast to the smaller colonies present during the second year of decay.

The subcortical fauna was similar to that of two-year-old logs, but *Dendroides bicolor* and *Synchroa punctata* were present in greater numbers. The larvae of these insects were usually the first animals that were seen when the bark was pulled from a log.

In parts of logs where no phloem-feeder had been, there was often a thick mat of fungus mycelia, probably of wood-rotting fungi, between the bark and wood. In such places several species of fungus beetles were found feeding on the fungi. As they ate out the fungus hyphae they formed small places between the bark and wood very much as phloem-feeders do in solid wood. Species found were the adults of *Platydema ruficorne, Haplocephala bicornis,* several unidentified coleopterous larvae, fly larvae, and the adults of staphylinids of the tribe Aleocharinae. In one instance a chelonethid, *Chelanops virginica,* was found eating a small larva. Small larvae that appeared from their structure to be predacious were also found. These were possibly staphylinids or histerids. The predacious larvae of *Alaus oculatus, Chariessa pilosa marginata, Philonthus* sp., and other unidentified species that appeared to be predacious from their large heads and long sharp mandibles, were common under bark. Adults of several predacious staphylinids and histerids were found. Centipedes of several species were common. Ants were found in every log, either under the bark, or running over the log. They probably feed on small larvae and various animal remains (Wheeler, 1913). Chelonehtids were found rarely.

Logs Over Three Years Old

As mentioned previously the sapwood of an oak log is fairly well rotted by the end of the third year. Following this there seems to be a period of several years during which the sapwood disintegrates further and eventually both the bark and sapwood begin to weather away. It was not possible to follow these stages in logs of known ages. Thus, logs in which the heartwood had begun to rot were selected for study in order to learn the animals associated with this stage of decay. Some of the logs studied had patches of the bark remaining, and others that were probably older consisted of a mass of rotten heartwood, with various amounts of solid heartwood as a core. The observations were based on logs that appeared to have been solid when felled. Trees attacked by heart-rot before they were cut would naturally disintegrate more rapidly. The heartwood in the logs examined had been attacked by "red-rot" fungi. Rotten wood of this type could be crumbled with the hands.

Twenty logs were examined and 96 species of animals were collected. Various groups were represented by the following number of species: Insects, 68; Chilopoda, 4; Diplopoda, 4; Acarina, 9; Chelonethida, 1; Annelida, 1; Mollusca, 7; Vertebrata, 1. Insecta were represented by the following orders with the number of species indicated: Collembola, 3; Thysanura, 1; Orthoptera, 1; Isoptera, 1; Coleoptera, 48; Diptera, 5 +; Lepidoptera, 1; Hymenoptera, 8. All these animals may be classified according to their food habits as follows: feeding on rotting wood, 30; feeding on fungi, or disintegrated wood under bark or beneath logs, 39; predacious, 25; nesting in rotting wood, 1.

The most characteristic animals were those feeding on rotting wood. The presence of many of the species listed apparently depended on a coverage of bark which was often lacking. The rotten wood caterpillar, *Scoleocampa liburna*, occurred in only two logs in which a small amount of sapwood remained. This is in contrast to its common occurrence in rotten sapwood in logs up to three years old. The scarabid, *Polymoecus brevipes* was found in large numbers in very rotten logs. In a log about 50 cm. in diameter and 10 meters long, it was estimated that there were about 150 larvae to the cubic meter. Larvae of another scarabid, *Trichiotinus bidens*, were found in two logs. The large larvae of a lucanid, *Pseudolucanus capreolus*, were found in nearly every log examined. In some cases they were under a log where they had formed small earthen cells. Another lucanid found as a larva was *Dorcus (brevis?)*. Only two were collected. Lucanids found as adults in rotting wood were *Ceruchus piceus* and *Platycerus quercus*. Larvae of the prionid, *Derobrachus brunneus*, varying in length from 1.0 to 7.0 cm. were found in rotting heartwood of eight logs. Larvae of *Xylopinus saperdoides* were common. Larvae of *Meracantha contracta* were found in very soft wood on the underside of logs. The small active larvae of an alleculid, *Hymenorus* sp. were common in heartwood attacked by "red-rot" fungi.

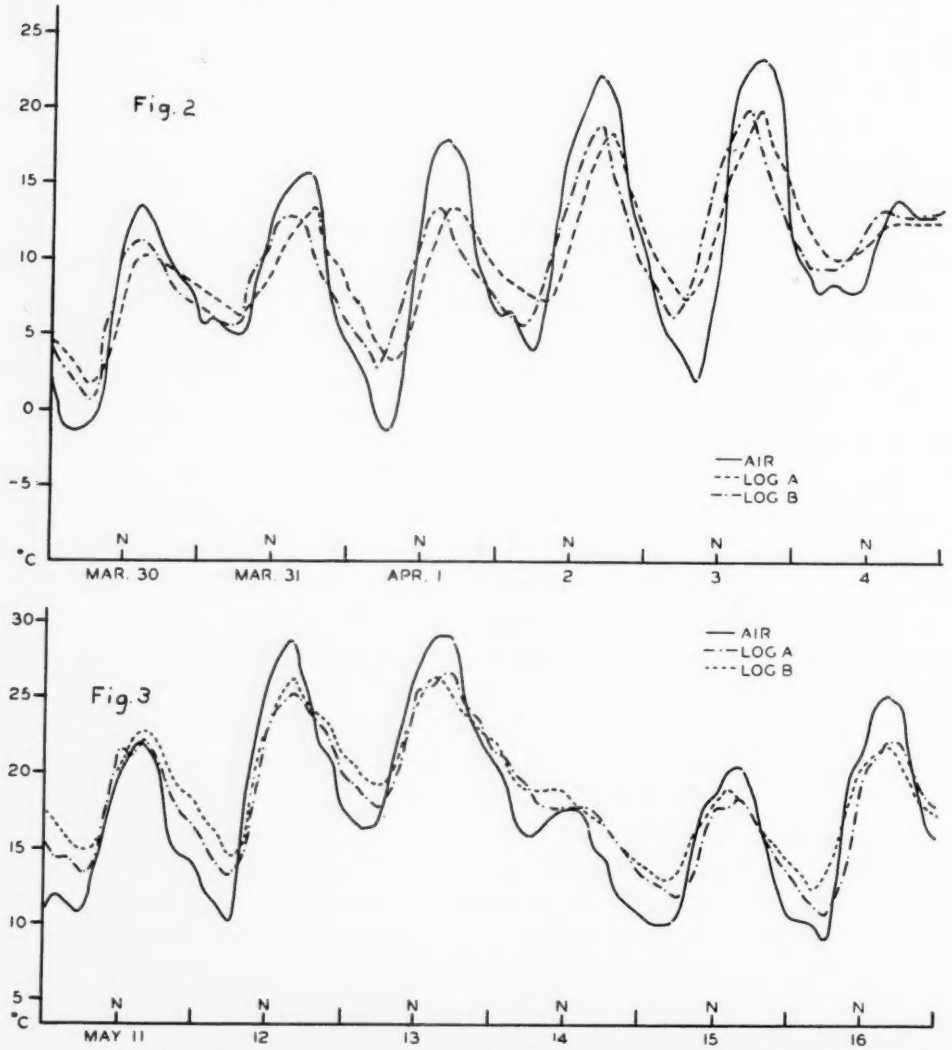
Probably the most important predacious animal was the larvae of an elaterid, *Alaus oculatus*. It will be noted that the presence of this species in logs of all stages has been mentioned. In the latter stages of decay it was observed feeding on *Pseudolucanus capreolus*. Adults and pupae were found in the burrows of *Derobrachus brunneus*. Probably it also feeds on the many larvae of *Polymoecus brevipes* that are often present, and on other large wood-boring larvae.

MICROCLIMATE

TEMPERATURE

The subcortical temperature in two-year-old pine logs exposed to the sunlight in August was considerably higher than air temperature (FIG. 4). The mean daily maximum temperature under the loose pine bark, 1 cm. thick, for the period August 3-9, 1937, was 43.2°C., whereas the mean daily maximum temperature in air for the same period was nearly 10°C. less. The

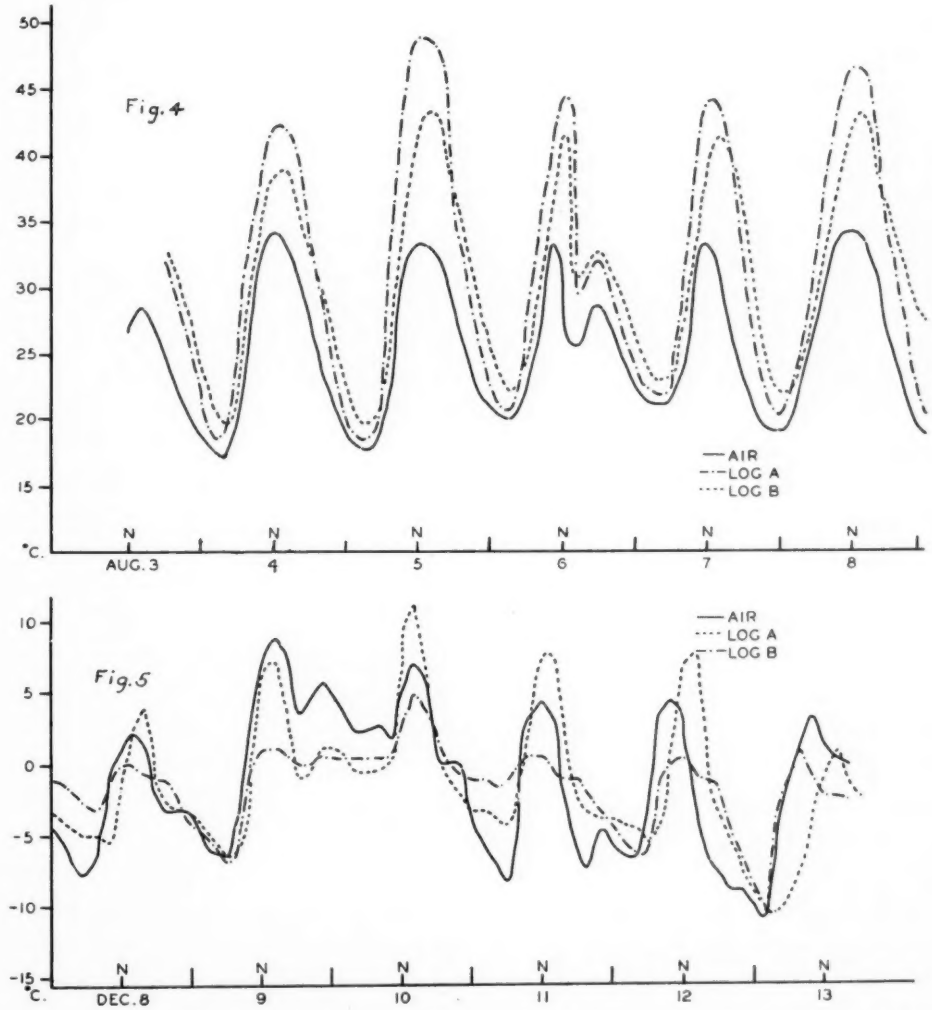
mean weekly temperature under the bark and in air for this period was 28.1 and 25.4°C., respectively, the difference being 2.7°C. The highest temperature recorded under loose pine bark was 48.9°C. when the air temperature was 33.3°C. The minimum daily temperature under loose bark in air was very nearly the same.



FIGS. 2-3. **2:** Temperature record in a pine log about 30 cm. in diameter that was one year old. The bark was about 1.5 cm. thick. "Log A," temperature in the sapwood at a depth of 5 cm. from the bark on the upper side. "Log B," temperature in the sapwood of the same log at a depth of 2 cm. from the bark on the upper side. **3:** Temperature record in an oak log about 30 cm. in diameter that was one year old. The log was lying north and south in the shade. The bark was about 1.0 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature in the same log, 2.5 cm. deep in the sapwood on the top side.

In pine logs exposed to sunlight in December, the rise of subcortical temperature over air temperature was evident but not as pronounced as that in August. During this period the highest temperature recorded under bark

was 12.1°C. when the air temperature was 7.2°C. The temperature record for December 8-14, 1937 (FIG. 5) is representative of the type of records obtained from November 30 to December 28.



FIGS. 4-5. **4:** Temperature in pine log, about eight months old, lying north and south in full sunlight. The bark had been loosened by bark beetles and cerambycids, and was about 1.0 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature under the bark of a pine log of the same age and in the same position. The bark was about 3.0 cm. thick. **5:** Temperature in a pine log, exposed to sunlight. The bark was loose and about 2.5 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature 2.5 cm. deep in the sapwood on the top side of the same log.

Temperature in all logs in shade fluctuated with air temperature in all seasons of the year, but the temperature under the bark or in sapwood of a log did not reach the maximum or minimum temperature recorded in air. The mean temperature in both air and in a log over a given period, however, was very nearly the same. The temperature record for the week March 30-

April 5 (FIG. 2), for example, shows that the mean maximum temperature under the bark of a two-year-old pine was 3°C. lower than that in air. During the same period the mean minimum temperature under the bark was 2.6°C. higher than in air. The temperature record obtained May 11-17 in a rotten oak log is also shown (FIG. 2) as an example of those obtained in logs in shade.

In records made of subcortical temperature in one-year pine logs in December, 1937, the daily minimum temperature under bark or 2.5 cm. deep in the sapwood, and in air were on some days very close together, while on other days they differed by several degrees. It will be seen in FIGURE 5 that on December 11, 1937, the minimum temperature 2.5 cm. deep in the log was —1.5°C. while the minimum air temperature was —8.9°C. The minimum temperature under the bark of the same log was at the same time about —3.9°C. Two days later when the air temperature fell to —11.1°C., the temperature both under the bark and 2.5 cm. deep in sapwood was —10.5°C. During this time the thermograph bulbs in the log had not been disturbed. On December 9 there also was little difference in the minimum air temperature and the temperatures in the same log, the temperatures at both depths in the log and in air being about —6.6°C.

AIR IN LOGS

Eleven samples of air taken from under the bark of oak and pine logs in October and December, 1937, showed from 0.24 to 1.83 per cent carbon dioxide by volume. These samples were taken by boring a hole through the bark and inserting a needle to draw out gases by the method previously described. It is probable that some contamination of the samples resulted. Another series of samples was collected in June, 1938, from a series of logs in which tubes had been rigidly emplaced for connection to the sampling apparatus. Percentages of carbon dioxide as high as 5.53 were found (Table 1). The decrease in the oxygen content of the samples from that of air was approximately equal to the increase in carbon dioxide content. The location of the ten tubes from which samples were taken follows:

TABLE 1. ANALYSIS OF AIR IN LOGS.

Log No.	CO_2%	O_2%	CO_2+O_2%	Log No.	CO_2%	O_2%	CO_2+O_2%	Log No.	CO_2%	O_2%	CO_2+O_2%
1	2.97	18.61	21.48	4	0.23	20.04	20.22	7	11.97	9.39	21.36
1	3.26	17.87	21.13		1.48	20.24	21.72		4.52	17.07	21.59
1	1.20	20.19	21.39		1.77	18.35	20.12		4.96	16.01	20.97
1	5.53	15.53	21.06	5	0.72	19.86	20.58	8	2.28	17.88	20.16
1	4.95	16.68	21.23		1.12	19.94	21.06		0.94	20.06	21.00
2	0.45	.....	.....		0.69	20.13	20.82	9	2.53	18.89	21.42
2	0.79	19.71	20.50	6	0.63	20.38	21.01		2.68	18.33	21.01
3	0.58	20.23	20.81		0.25	21.88	22.13	10	0.89	19.45	20.34
3	0.20	20.78	20.98		0.44	20.52	20.96		1.95		

No. 1—Under the bark on the top side of an oak log four years old and about 40 cm. in diameter. The sapwood under the bark was soft and the bark loose.

No. 2—Same log as No. 1. Tube ran through sapwood into the punky heartwood about 60 cm. from end of log.

No. 3—Same log as No. 1. Tube inserted to depth of about 30 cm. into the center of the end of log. All heart was rotten and punky. Passalus working around tube.

No. 4—Under bark on top side of a pine log one year old, about 25 cm. in diameter. Exit holes of buprestids and cerambycids were plugged for radius of about 10 cm.

No. 5—Hole bored into the end of a three-year-old pine log about 25 cm. in diameter. Sapwood was rather solid but had been attacked by fungi leaving pores through the wood.

No. 6—Tube under the bark of pine log one year old and about 30 cm. in diameter.

No. 7—Under bark and one inch into sapwood of a pine log three years old. Log about 75 cm. in diameter.

No. 8—Tube 30 cm. into the end of a pine log two years old.

No. 9—Tube inserted into a Passalus burrow under bark of an oak log about four years old. Log about 75 cm. in diameter.

No. 10—Same log as No. 9 on the top under the bark. The bark was loose and perforated by cracks and exit holes of beetles.

MOISTURE IN LOGS

The moisture content of the 69 logs tested varied widely during the spring and summer. Those that consistently had a low moisture content were small poles that were rotten and exposed to sun. Values for these logs ranged from 26 to 53 per cent. The moisture content shortly after rains was naturally greatest. Logs that were punky took up water quickly since the wood was very porous and the bark was either perforated in many places or lacking. Moisture content of such wood was as high as 372 per cent. Often various logs that had been cut only one year showed moisture contents up to 60 per cent after rains, and logs two years old contained as much as 198 per cent. Throughout the spring and summer of 1937 when samples were taken none were found that contained less than 50 per cent moisture except the pine poles previously mentioned. The frass under the bark of pine logs the first summer after they were cut contained from 102 to 293 per cent moisture.

These results are presented only to show the variation in moisture content of some representative logs from which collections were made and do not represent a comprehensive survey of logs under all conditions. Since most of the collections were made from logs in the forest it is to be ex-

pected that moisture contents found are higher than would be found in logs in open situations exposed to more sunlight.

TOLERATION OF HIGH TEMPERATURES

In the experiments on thermal death points at different relative humidities, the following larvae were investigated:

Cerambycidae	*Romaleum atomarium* (Drury)
	Monochammus titillator (Fab.)
	Acanthocinus nodosus (Fab.)
Buprestidae	*Chrysobothris* sp. (probably femorata Oliv.)*
Pyrochroidae	*Dendroides bicolor* (Newm.)

Larvae were collected one to three days before they were used, and kept at room temperature in one-ounce metal cans with some of the wood from which they were collected. To determine the amount of water lost, the weight of the feces deposited during an experiment was deducted from the total weight lost. In experiments on larvae of *Acanthocinus nodosus* and *Chrysobothris* sp., a Warburg apparatus was used. The other larvae were tested in jars in a water bath.

TABLE 2. RESULTS OF EXPOSING LARVAE OF *Chrysobothris femorata* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
3	50	Alive	4	50	Alive
4	51	Alive	3	51	Alive
4	52	3 alive, 1 dead	4	52	2 alive, 2 dead
4	53	Dead	4	53	Dead

Chrysobothris sp. larvae (Table 2), collected on August 5 and 6, 1937, from the bark of white oak logs in which they had formed hibernating cells, survived at temperatures as high as 52°C. when the humidity was either 10-15 or 90-95 per cent. The average loss of water for four individuals under each of these conditions was 8.6 and 2.4 per cent respectively.

Larvae of *Monochammus titillator* (Table 4), collected August 9 and 12, 1937, from under pine bark survived a temperature as high as 50°C. when the relative humidity was 10-15 per cent, with an average loss of water for three individuals of 26.9 per cent. In humidities of 50 per cent larvae survived at 49°C., with an average water loss for three individuals of 17.7 per cent. In a saturated atmosphere larvae only survived temperatures as high as 44°C. with no loss of water.

* The larvae of Chrysobothris have not been sufficiently described to make accurate determinations possible. *Chrysobothris femorata* has been reared from several logs, and the larvae of that species appear to be similar to those used in these experiments.

Larvae of *Romaleum atomarium* (Table 3), collected from oak logs and stumps September 4 and 5, 1937, survived a temperature of 49°C. when the relative humidity was 10-15 per cent, with an average water loss for four individuals of 26.9 per cent. They survived temperatures of 46°C. when the relative humidity was 50 per cent, and lost 12.7 per cent of their body weight. In a saturated atmosphere, 45°C. was the highest temperature tolerated.

Acanthocinus nodosus (Table 5), collected from under pine bark September 14, 1937, endured temperatures as high as 46°C. when humidity was at 10-15 per cent, with an average loss of water amounting to 16.1 per cent. When humidity was 90-95 per cent, 44°C. was the highest temperature at which they survived, the corresponding water loss amounting to 1.7 per cent.

Larvae of *Dendroides bicolor* (Table 6), collected under bark of rotting oak logs, survived at temperatures as high as 41°C. when humidity was either 10-15, 50, or 100 per cent. Under these conditions they lost 19.1 per cent of their body weight by evaporation of water in 10-15 per cent humidity; 14.5 per cent at 50 per cent humidity; and 0.0 per cent in a saturated atmosphere.

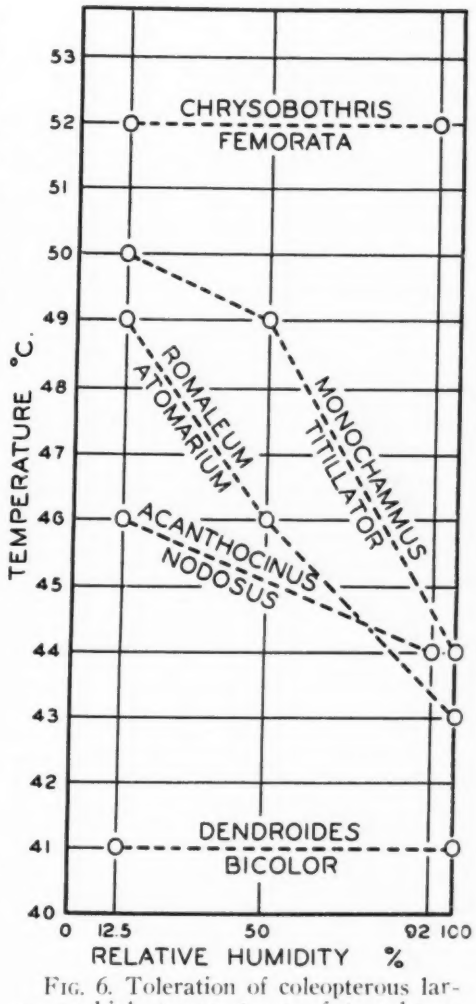


FIG. 6. Toleration of coleopterous larvae to high temperatures of two hours duration in atmospheres of different humidities. Each point represents the highest temperature tolerable.

TABLE 3. RESULTS OF EXPOSING LARVAE OF *Romaleum atomarium* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	45	Alive	3	46	2 alive, 1 dead	8	43	Alive
3	46	Alive	2	48	Dead	4	45	Dead
4	48	Alive	4	49	Dead	2	46	Dead
4	49	3 alive, 1 dead	8	50	Dead			
8	50	Dead						

TABLE 4. RESULTS OF EXPOSING LARVAE OF *Monochammus titillator* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	44	Alive	2	46	Alive	8	43	Alive
3	46	Alive	3	49	Alive	4	44	2 alive, 2 dead
3	49	2 alive, 1 dead	3	50	Dead	2	49	Dead
3	50	2 alive, 1 dead	4	51	Dead	2	50	Dead
4	51	Dead						

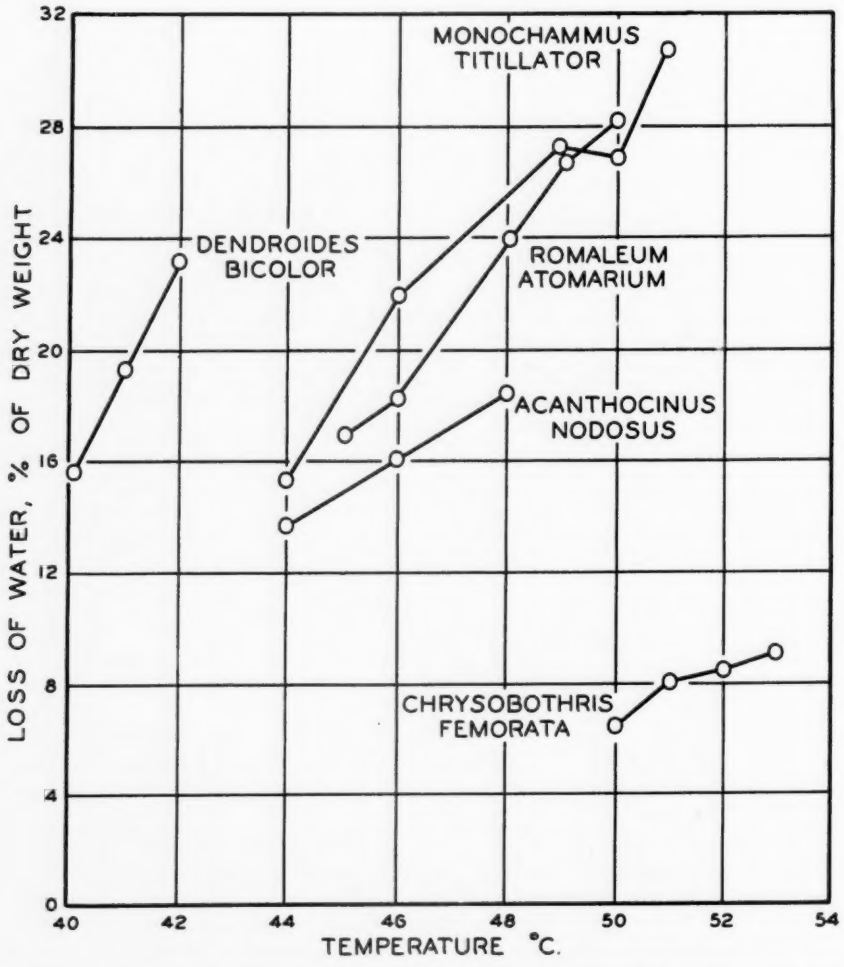


FIG. 7. Relation between temperature and the percentage body weight lost as a result of evaporation of water by various coleopterous larvae. Larvae were exposed for two hours in an atmosphere of 10-15 per cent relative humidity (Table 7).

TABLE 5. RESULTS OF EXPOSING LARVAE OF *Acanthocinus nodosus* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	44	Alive	2	48	Dead	8	43	Alive
4	46	Alive				4	44	1 alive, 3 dead
4	48	Dead				4	46	Dead
						2	48	Dead

TABLE 6. RESULTS OF EXPOSING LARVAE OF *Dendroides bicolor* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
3	40	Alive	3	40	Alive	3	40	Alive
3	41	Alive	3	41	Alive	3	41	Alive
4	42	Dead	2	42	Dead	3	42	Dead

It will be observed that *Chrysobothris* sp. with the highest thermal death point lost less water than any of the other species. Larvae of *Dendroides bicolor* lost more water than the other species in relation to the temperature to which they were subjected (Table 7, FIG. 7). Toleration of all larvae to high temperatures is presented in FIGURE 6.

TABLE 7. RESULTS OF EXPOSING LARVAE IN HUMIDITY OF 10-15 PER CENT AT VARIOUS TEMPERATURES FOR TWO HOURS.

Upper figure, temperature; lower figure, loss in body weight (in per cent) from evaporation of water.

Chrysobothris femorata	50° 6.3	51° 8.1	52° 8.6	53° 9.2	
Monochammus titillator	44° 15.2	45° 22.1	49° 27.3	50° 26.9	51° 30.7
Romaleum atomarium	45° 17.0	46° 18.6	48° 24.1	49° 26.9	50° 28.3
Acanthocinus nodosus	44° 13.9	46° 16.1	48° 17.5		
Dendroides bicolor	40° 10.3	41° 14.5	42° 14.7		

FOOD RELATIONS

In order to learn what foods were eaten by insects in logs, the gut contents of certain species were examined. Species that were obviously boring in wood were not examined. In some cases, it was doubtful as to whether

a species was predacious or feeding on fungi when it was found under bark, and it was to such species that more attention was given. In the following paragraphs the results of the examinations are given.

Tachymenis flavicauda Say (Carabidae), 10 adults. Fragments of mites and collembolans were found in the gut. The legs of mites of the families Uropodidae and Trombidiidae could be identified. Collembolan remains consisted of antennae, scales, parts of the furcula, and legs. This species is common under pine bark.

Tachyta nana (Gyll) (Carabidae), 10 adults. Contents of the gut of these carabids were similar to those of *Tachymenis flavicauda: Tachyta nana* is common under oak bark.

Cossonus corticola Say (Curulionidae), 8 adults. Collected from under pine bark where they are common. Fungus hyphae and spores were found in the gut.

Canosoma crassus Grav. (Staphylinidae), 5 adults. This staphylinid was common under oak bark. Only fungus hyphae and spores were found in the gut. Two individuals contained only round black spores. The others had about 50 per cent hyphae and 50 per cent spores of various shapes.

Platysoma lacontei Mars. (Histeridae), 10 adults. Found under oak bark. Food in the gut appeared to be entirely of animal origin. Individuals were confined with fly larvae with which they were associated under the bark. The fly larvae were eaten in every case. Two individuals ate six fly larvae in one day.

Ecritus exiguus (Er.) (Histeridae), 3 adults. These small histerid beetles were found under oak bark. Only black fungus spores were found in their guts.

Saprinus sp. (Histeridae), 6 larvae. The gut contents of these larvae showed that food was of animal origin. A few fungus spores and particles of wood were found in four specimens. It is probable that these were taken in with other food. Saprinus larvae were common under pine bark where there were many dipterous larvae. Three of them were confined with six of the dipterous larvae and at the end of 24 hours all of the latter had been eaten. The shriveled integuments of the fly larvae remained, showing that the soft parts of their bodies had been eaten.

Cylistix cylindrica (Payk) (Histeridae), 10 adults. Only an oily liquid, probably of animal origin, was found in the gut. The insects occurred under pine bark where there were many fly larvae. When confined with some of these fly larvae (probably *Lonchaea* sp.) they ate them readily.

Thanasimus dubius (Fab.) (Cleridae), 10 adults. Adults collected from pine that contained many scolytids under the bark. *T. dubius* was seen catching and eating adults of *Ips calligraphus* on logs. In the laboratory it would immediately attack and eat out the soft parts of the adults of that little

beetle placed with them. The gut contents of the ten adults collected from logs consisted entirely of animal matter.

Dendroides bicolor Newn. (Pyrochroidae), 20 larvae. Fungus hyphae and spores made up approximately 90 per cent of the gut contents. The rest consisted of particles of wood and liquid.

Ischiodontes sp. (Elateridae), 10 larvae. The larvae of this elaterid were found under pine bark. Only particles of wood with a few fungus hyphae and spores were seen in the gut contents.

Alaus, 10 larvae, from pines and oaks. (*Alaus myops* is found in pines and *A. oculatus* in oaks.) An oily chyme in which a few small particles of wood and fungus spores were sometimes found. Larvae brought to the laboratory ate any kind of larvae placed before them. In the field they were observed feeding on the larvae of *Monochammus titillator*, *Derobrachus brunneus*, *Pseudolucanus capreolus*, *Polymoecus brevipes*, *Alobates pennsylvanica*, and *Romaleum atomarium*.

Temnochila virescens (Ostomidae), 10 larvae. The gut contents consisted of an oily chyme, indicating that animal food had been eaten. A few particles of wood were found in some larvae. Observations on the feeding habits of these larvae show that they are general feeders. They were found in the pupal cells made in the sapwood by *Monochammus titillator* where the partially eaten larvae of that beetle gave evidence of their predatory habits. The larvae of *T. virescens* was also found in the pupal chambers formed by *Callidium antennatum* and *Chrysobothris* sp. in pine poles. In such cases it could be seen that the larvae of *T. virescens* had tunneled through the burrow of these borers, apparently to search them out and eat them. In certain empty pupal chambers that could not be accounted for by the emergence of the wood borers or by the attack of a parasite, a small burrow, apparently made by *T. virescens*, was seen leading from the frass left by the borer to its pupal chamber in the sapwood.

Brontes dubius Fab. (Cucujidae), 9 adults, 1 larva. Occurs under pine and oak bark. In both adults and larvae only fungus hyphae and spores were present.

Silvanus planatus Germ. and *S. imbellis* Lec. (Cucujidae), 15 adults. These cucujids are common under oak bark. In both species fungus hyphae and spores were found. Certain cucujids are supposed to be predacious, but apparently these are not, at least in the adult stage.

Uloma punctulata Lec. (Tenebrionidae), 5 adults, 2 larvae. Common in rotten pine wood. In both larvae and adults, rotten wood was in the gut.

Uloma imberbis Lec. (Tenebrionidae), 6 adults. A species similar to *U. punctulata*, but found in rotten oak. Only rotten wood was found in the gut.

Platydema subcostatum Lap. (Tenebrionidae), 6 adults. Found in groups under oak bark, feeding on patches of mold. Hyphae and spores were found in the gut.

Platydema ruficorne Stunn. (Tenebrionidae), 4 adults. Found under oak bark, feeding on fungi. Hyphae and spores were found in the gut.

Boros unicolor Say (Boridae), 2 larvae. The gut contents of the larvae examined consisted of particles of wood and fungus hyphae and spores. No estimates of the relative amounts could be made. It appeared that the particles of wood contained much of the fungus hyphae. Larvae occur under the bark of pine where they feed in the frass left by various phloem-feeders.

Synchora punctata Newn. (Melandryidae), 10 larvae. Gut contents consisted entirely of bits of wood intermeshed with fungus hyphae and spores. The relative amounts could not be estimated.

TESTS FOR CELLULASE

The gut contents of larvae of eleven species of wood-eating insects were tested for the presence of a cellulase by the methods previously described. Larvae were feeding in every case when they were taken from the logs for tests, except those of *Derobrachus brunneus,* which were collected in winter. They began to eat, however, after they were left in room temperature for several days. The following is a list of the species used, with the number of larvae investigated and the type of wood they ate:

Passalidae	*Passalus cornutus* Fab., 10. Feeds on rotten wood of various deciduous trees and rarely pine.
Lucanidae	*Pseudolucanus capreolus* L., 6. Feeds on rotting pine and deciduous trees.
Scarabidae	*Polymoechus brevipes* Lec., 15. Larvae collected from oak log rotted by "red-rot" fungi.
Cerambycidae	*Derobrachus brunneus* (Forst.), 12. Feeding in rotting pines and hardwood. Larvae were also found in the solid heartwood of a rotting oak log.
	Rhagium lineatum Oliv., 6. Feeds in phloem of pines.
	Callidium antennatum Newm., 8. Feeds in phloem of pines.
	Romaleum atomarium (Drury), 13. Feeds in phloem of oaks and in rotting oak wood.
	Monochammus titillator (Fab.), 12. Feeds in phloem of pines.
	Acanthocinus nodosus (Fab.), 8. Feeds in phloem of pines.
Tenebrionidae	*Alobates pennsylvanica* (Degeer), 12. Found in rotting oak.
Noctuidae	*Scolecocampa liburna* Geyer, 5. Found in rotting oaks.

The only positive test for a cellulase in this series of larvae was obtained with the gut contents of *Derobrachus brunneus.* The larvae were collected February 14, 1938, from a very rotten log. They had formed burrows in

the heartwood that was still hard. The juice from their gut had no apparent action on wood shavings or filter paper, but digested a section of lettuce midrib completely in four hours.

AMOUNTS OF WOOD EATEN BY *Callidium antennatum* AND *Chrysobothris* SP. IN PINE

Examination of Frass

The frass in the burrows of both *C. antennatum* and *Chrysobothris* sp. was fine and tightly packed. Its predominant color was that of the sapwood. Scattered through the frass were dark brown particles that on closer examination proved to be fecal pellets. These pellets were the same color as the phloem, which was brown in a log that had dried out. When they were soaked in water and pulled apart with needles, it was found that they were made up of many fine particles of wood that were cemented together. These particles could be identified as phloem. Close examination of the lighter colored particles which made up the greater part of the frass showed them to be clean cut, individual chips of sapwood. Their size varied, being larger toward the end of the burrow where the mature larva was found.

AREA OF THE BURROW AND DRY WEIGHT OF LARVAE

The average dry weight of the phloem covering area of one square centimeter on shortleaf pine trees was found to be 0.0555 ± 0.0021 grams. This figure is based on ten samples taken from shortleaf pines, about 25 cm. in diameter, that had been cut for a week. Five samples were taken at one meter from the base of the tree and five at about 10 meters from the base.

All the larvae of *Callidium antennatum* examined had constructed their cells in the sapwood and had completed their feeding period. The areas of the ten burrows examined ranged from 22.6 cm.^{2} to 60.7 cm.^{2} The dry weights of the larvae from the same burrows ranged from 0.0158 gm. to 0.0422 gm. Their wet weight ranged from 0.0584 gm. to 0.1512 gm., the percentage of body weight lost in drying varying from 49.36 to 79.75 per cent. The estimated amount of wood eaten by the larvae ranged from 1.26 ± 0.10 to 3.37 ± 0.26 grams (FIG. 8). Expressed in terms of grams of wood per gram of larvae the amounts consumed varied from 75.60 ± 6.0 gms. to 79.81 ± 6.2 gms., the average being 77.9 ± 3.2 gm.

The areas of the five burrows made by larvae of *Chrysobothris* sp. ranged from 6.97 cm.^{2} (an immature larva) to 25.74 cm.^{2} The larvae weighed before drying 0.0178 gm. (an immature larva) to 0.1014 gm. After being dried they weighed from 0.0048 to 0.0260 gms. The estimated amount of wood eaten ranged from 0.39 ± .03 gms. to 2.06 ± .16 gms. (FIG. 8). The amount of wood eaten expressed as grams of dry wood per gram of dry larva ranged from 75.07 ± 5.8 to 50.56 ± 6.3, averaging 79.0 ± 3.1 grams.

The estimated amount of wood consumed by the larvae of both species was proportional to the areas of the burrows (FIG. 8). It will be noted that the amount of wood eaten per gram of larva fell within a narrow range in the larvae of both species. If a population of *C. antennatum* is assumed in which mature larvae contain 68.4 per cent water (the average of the ten determined) then an area of one square foot (929 cm.^{2} or 0.0929 m.^{2}) of log, having a phloem layer comparable to that determined in this experi-

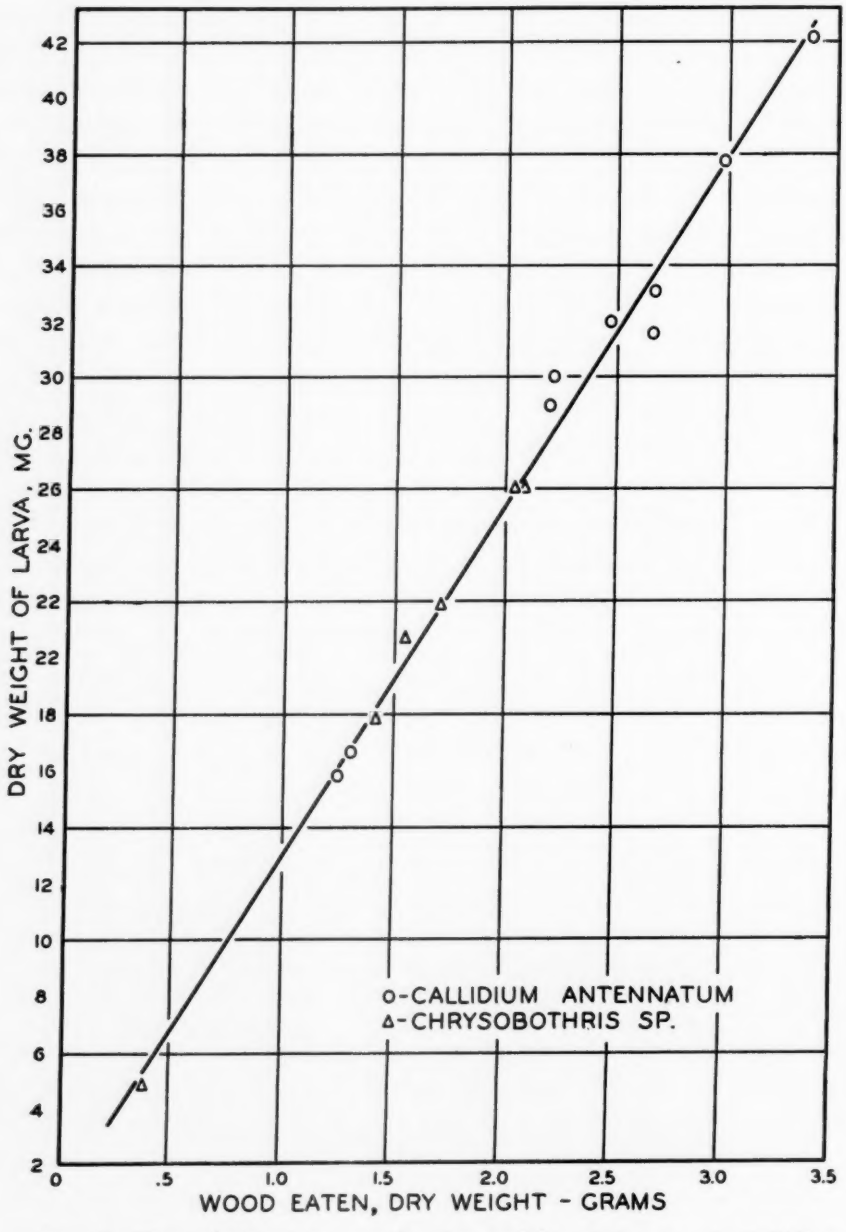


FIG. 8. The relation between the dry weight of larvae of *Callidium antennatum* and *Chrysobothris* sp. to the calculated amount of dry phloem that they consumed.

ment, would have the potentiality of producing 2.2 grams of larvae (wet weight) if all the available phloem were utilized. Assuming the average wet weight of a mature larva to be 0.1 grams this would give 22 individuals to the square foot.

None of the log from which larvae were collected showed starch in the sapwood with the potassium iodide test. The inner bark (cambium) layer, however, showed an abundance of starch as evidenced by the deep blue-black color produced. These observations were confirmed by microscopic examination of thin sections of wood treated with iodide solution. Large blue granules of starch could be seen in certain cells of the phloem while none could be found in the sapwood. Special attention was directed to parenchyma cells of rays and resin ducts in the sapwood which are known to be storage cells, but in no case was starch found. A freshly cut pine log was examined in March, 1938, and did show a small amount of starch in the parenchyma cells of the rays and resin ducts. Thus the previous findings only apply to the logs examined and are not to be taken as representing the conditions to be expected in any pine log. In no case was starch found in fecal pellets that had been picked from the frass and treated with iodide solution.

ANALYSIS OF WOOD

Samples of living phloem from three shortleaf pine trees *(Pinus echinata)* cut in November, 1937, contained an average of 5.02 per cent (dry weight) starch. Duplicate determinations were made on three samples with the following results: (1) 4.82 and 4.97 per cent, (2) 4.86 and 5.21 per cent, and (3) 5.10 and 5.18 per cent.

DISCUSSION

SUCCESSION

Pine. There is a succession of animals in pine logs similar in nature to that described by Adams (1915) and Blackman and Stage (1924). The first animals entering a log are cerambycid, burprestid, and scolytid beetles. All of these animals feed on phloem. It has been shown that scolytids and certain cerambycids aid the entrance of wood-rotting and other fungi in logs (Leach, Orr, and Christensen, 1937). The activity of these animals leaves a space under the bark more or less packed with chewed-up wood, part of which has been through the gut of some larva. Apparently such conditions are favorable for the growth of various fungi other than those that contribute to wood decay. These phloem-feeding animals therefore help to change the condition of a log so as to make it attractive to a large number of species that feed on fungi and decaying wood. Most of the members of the phloem fauna in pines complete their life cycle in one season or less. By the end of the first summer after a pine log is cut, there is usually little or none of the phloem remaining. This is only the case if a log is not exposed to unusual

conditions, such as being split and racked where it can be dried out rapidly. Logs in contact with the ground or in partial shade invariably contain many insects feeding on phloem. During the second year the sapwood begins to become softened and species that feed on such wood enter. The subcortical fauna is still very much the same with the addition of certain species such as *Dendroides bicolor* and *Boros unicolor*. During the third year additional species enter the sapwood, which by this time is often punky in places. The bark on small logs has often fallen off. Where it remains, the subcortical fauna typical of the first and second year is present, but represented by fewer species. After the sapwood has become punky throughhout, fewer species are found in it, and species characteristic of intermediate stages of decay are absent, or are only rarely found. One species found in such wood, *Derobrachus brunneus*, is able to digest cellulose. The final stages in the decomposition of the wood, in which it becomes a part of the soil has not been studied, but it is reasonable to assume that insects characteristic of the soil fauna (termites, etc.) replace those found only in rotten wood.

Oaks. The succession of animals in oak logs is essentially the same as that in pine logs in that the same ecological groups of animals are involved. There is first a phloem-feeding fauna that prepares the way for the entrance of a subcortical fauna living on decayed wood and fungi. In oak logs the entrance of a subcortical fauna is not entirely dependent on the phloem-feeders as it appears to be in pine. The bark of oak logs may become loosened sufficiently for the entrance of some insects merely by the drying of the phloem layer. Species feeding on solid wood, on wood in early stages of decay, and on punky wood succeed each other. Some species such as *Passalus cornutus* are among the first to enter a rotting log and remain until it is beginning to fall apart. Certain species such as *Uloma imberbis* and *Polymoecus brevipes* appear to select wood attacked by "red-rot" fungi while other species such as *Alobates pennsylvanica* appear to select wood attacked by "white-rot."

Oak logs in the punky stage of decay contain more species of animals and more individuals than does the corresponding stage in pine. The length of time required for the transformation of pine and oak logs from a solid log to a stage where they become mixed with the litter of the forest floor was not determined exactly. It appears, however, from the observations made on pine and oak logs three to four years old, that the decay of the former is much more rapid. The time required will naturally be influenced by the size of the log and the conditions to which it is exposed. Oaks have a relatively large amount of heartwood which is resistant to decay; pine logs contain relatively less heartwood. Thus, the decay of sapwood in a pine log affects a greater part of the log than would a corresponding amount of decay in the sapwood of oaks. Oak logs up to 60 cm. in diameter that had been dead over five years still contained solid heartwood. It appears that slowness of the decay of the large amount of heartwood in an oak log makes

for a suitable habitat for animals feeding in rotting wood for several years after sapwood and bark have decayed and weathered away.

While comparable ecological groups of animals occur in both pine and oak logs, the species are, for the most part, different. Closely related species of the same genus *Uloma punctulata* and *Uloma imberbis* occur in pine and oak respectively. In the genus Alaus, *A. myops* occurs in pines and *A. oculatus* occurs in oak. Both of these species are predacious and feed on a variety of wood-boring larvae. It is therefore difficult to understand why the two species should have a specific preference for a coniferous or a deciduous tree. Probably the answer is not to be found in specific wood preferences of the larvae, but in a strongly fixed oviposition response of the females to either a coniferous or a deciduous tree. Possibly *Alaus myops* and *A. oculatus* arose from xylophagous forms that had developed a preference for a particular host tree. Oviposition response of the female to a particular type of tree conceivably might have remained even after the larvae no longer fed on wood. *Xylopinus rufipes* was found only in pine and *X. saperdoides* only in oak. The small carabid, *Tachymenis flavicauda*, occurs in pine and a similar species, *Tachyta nana*, is found in oak. Both species feed on mites and collembolans.

Certain species are not restricted to either pine or oaks. About 25 species were found that occur in both types of trees. These include species feeding on rotting wood, on fungi under the bark, and on other insects. The large eletarid larvae *Orthosetethus infuscatus* occurs in rotten logs of both types of trees. *Derobrachus brunneus* also bores in both rotten pine and oak logs. Ants and centipedes are not restricted to one type of tree. Termites are equally common in both types of logs. *Brontes dubius* and certain staphylinids occur under the bark of both pines and oaks, where they feed mainly on fungi. *Dendroides bicolor* and *Synchroa punctata* may occur in both pines and oaks, but they are more commonly found in oaks. *Passalus cornutus* feeds typically in oaks and other deciduous trees, and rarely occurs in pine. Apparently no generalizations can be made concerning the species common to both types of logs. Weiss (1920a) has shown that certain fungi are attractive to more insects than others. Possibly a difference in the fungal flora of pine and oak logs may explain the preference of certain fungus-feeding insects for either pine or oak logs. Predators such as centipedes are of general occurrence both in litter and in logs and would not be expected to show a preference for particular species of trees.

Adams (1915) says that, in general, the fauna of rotting logs of different species of trees tends to become the same as they grow older. This is doubtless true of deciduous logs, but can hardly be applied to both deciduous and coniferous trees. While certain species are common to both rotten pine and oak logs, most of the species which feed on rotting wood are different.

When pine and oak logs have fallen apart, and are becoming part of the humus layer of the forest, probably more animals would be common to both.

Members of the phloem-feeding fauna are apparently the only animals whose activity prepares the way for succeeding animals.

Shelford (1911) says: "Ecological succession is the succession of ecological types (physiological types, modes of life) over a given point or locality due to changes in environmental conditions at that point. From this point of view we have nothing to do with species except as names are necessary." In a forest habitat the significant environmental changes which affect succession in a log are those caused by fungi and, to a lesser extent, the action of animals. The change is both chemical and mechanical and is probably most significant because of its relation to food requirements of animals. Logs are not everlasting habitats, but eventually merge with an adjacent habitat, the humus of the soil.

MICROCLIMATE

Temperature. Records of temperatures under the bark of logs exposed to sunlight in summer show that solar radiation has a marked effect on the subcortical temperature. The results obtained are similar to those reported by various other workers (Craighead 1920, Graham 1925, Patterson 1930, and Gottlieb 1928). High temperatures in logs exposed to the sun were shown by Graham (1925) to be of significance in shortening the time required for development of beetles. Subcortical temperatures may also be fatal to bark beetles, and advantage has been taken of this fact in control methods for certain bark beetles attacking pines (Patterson, 1930).

The subcortical temperatures recorded under pine bark on clear days in December show that solar radiation may raise the subcortical temperature above air temperature in winter. The effect of solar radiation in winter, however, is not as great as in summer. Certain animals living under bark such as collembolans, carabids, staphylinids, and dipterous larvae are not inactive all winter in the Duke Forest. All of these insects were active under bark when the subcortical temperature was above 7 to 10°C. In logs exposed to the sun the effect of solar radiation in raising the subcortical temperature as much as 5°C. above air temperature, enables such insects to be much more active.

The fluctuation of temperature in logs in shade with air temperature is to be expected since a log is of course subjected to changes in air temperature. The lag of temperature at various depths in logs accounts for the failure of log temperature to reach the maximum and minimum air temperatures, since the daily maximum and minimum air temperatures do not usually last more than an hour. When air temperature was fairly constant over a period of several hours, as it sometimes was in winter, temperatures in logs had time to come into equilibrium with air temperature. It is not likely that the maximum and minimum temperature under the bark of logs in the

shade and the maximum and minimum temperature of air differ sufficiently to be of great significance to animals living in such places during the summer, spring, and fall. The significance of the differences in the minimum and maximum temperatures under bark in winter and in air is questionable. From the records obtained on the days when air temperature was below 0°C. it appears that bark may sometimes offer protection to animals from sudden drops in temperature of short duration (FIG. 5), but low temperatures lasting as much as three to four hours are also reached under bark. There are many insects that hibernate under bark and crevices in logs. The protection afforded by bark to hibernating insects is thus very slight. Logs are probably more important as hibernacula on account of their high moisture content and the fact that they afford protection to various arthropods from birds, than on account of protection from low temperatures.

It was thought before temperature records were made that perhaps rotting logs would have a significantly higher temperature than air, because of the activity of bacteria and other fungi or because of auto-oxidative processes. In none of the records obtained can any such effect be shown. Any heat produced in the logs from these causes was not enough to raise the mean temperature of a log significantly above the mean air temperature. The disintegration of a log is a rather slow process, requiring several years, therefore heat produced by the activity of bacteria, fungi or auto-oxidative processes is probably conducted outward as fast as it is produced.

MOISTURE CONTENT OF LOGS

In all the logs from which collections were made, except certain pine logs that had been split and racked, the moisture content was well above that which would be expected to obtain in air-dry wood. Hawley and Wise (1926) give data to show the relationship between the moisture content of wood in equilibrium with atmospheres of different relative humidities at 24°C. While they state that the details of the relationship are not well worked out, especially at the extreme ranges of humidity, their results can be taken as approximately correct. According to their data, wood absorbs 33 per cent of its weight of water in a saturated atmosphere at 24°C. No work seems to have been done on the equilibrium that would be obtained between wood of different moisture contents and dry air. It is reasonable, however, to assume that when wood is in equilibrium with a saturated atmosphere, any air space in the wood would also be saturated. If wood contained more water than that which it would absorb from a saturated atmosphere, the humidity of air spaces in the wood should undoubtedly be close to 100 per cent since there is nothing to prevent water in the wood from exerting its normal vapor pressure. It seems safe to conclude therefore that wood containing as much as 50 per cent moisture would raise the humidity of a small, closed air space to the saturation point, provided of course, the volume of air be not too much greater than the volume of wood. Since most of the logs from which

samples of wood were collected contained 50 per cent or more water, any air space in such logs, as those made by insects, should be expected to be at or near to the saturation point at all temperatures.

As there is a lack of knowledge on the relation of wood moisture to humidity of air spaces in the wood, conclusions as to the humidity of the atmosphere in which *Callidium antennatum* and *Chrysobothris* sp. live cannot be drawn from the results of this research. The water content of the wood in which they live (relatively dry pine logs) was found to be as low as 26 per cent. According to data given by Hawley and Wise (1926) this corresponds to the amount of water contained in wood in equilibrium with an atmosphere of 95 per cent relative humidity. It seems likely that such a sample of wood would maintain a humidity in its contained air spaces greater than the usual atmospheric humidity, and would be free from the variations occurring in atmospheric humidity.

From the data obtained it appears that logs that have been attacked by wood-rotting fungi are capable of containing more water than freshly cut logs. This can be explained by the fact that the fungi break down and remove part of the wood, leaving more spaces to hold water.

Moisture is undoubtedly of great significance to many animals living in logs. Relative humidities of less than 100 per cent are fatal to many collembolans (Davies, 1928). Soft-bodied nymphs of many species of mites living under bark are probably similar to collembolans in their requirements for moisture. Larvae of *Dendroides bicolor,* which are typical subcortical animals, were shown by the writer to be sensitive to low humidites. The common observation that dry logs do not contain many wood borers also indicates that moisture in logs is important. Fidler (1936) showed that the moisture content of the soils was of great importance to the larvae of a scarabid. Not only do they require an atmosphere of saturated humidity, but also soil containing more water than would be necessary to maintain a saturated humidity in soil air. It seems probable that larvae of scarabids and lucanids living in logs might have similar reactions to the moisture content of wood.

CARBON DIOXIDE IN LOGS

The data on the presence of carbon dioxide in air under the bark and in wood of logs indicates that the composition of the atmosphere in which log-dwelling animals live may be quite different from the normal composition of air. The scope of the data collected is not great enough to determine the conditions under which carbon dioxide would be most abundant or the maximum amounts that might be expected. It does seem that greater amounts should be obtained during warm weather when the activity of bacteria and fungi would be greater, and that the greatest amount should be expected where fungus growth is most abundant. Many openings in the bark should also be expected to increase ventilation and thus influence the amount of

carbon dioxide found under the bark. High temperatures and wind would be expected to cause a greater diffusion of carbon dioxide from a log, since these factors are of importance in the ventilation of soil (Keen, 1931). The effect of carbon dioxide in the concentration found, or in higher concentrations that might be present, on insects living under bark or in the wood of logs, has not been studied to the writer's knowledge.

Carbon dioxide is important in controlling the respiration of some insects. It has been shown that *Dixippus morosus* responds to carbon dioxide with an increased rate of respiratory movement. This response shows two maxima, one between 0.0 and 1.0 per cent carbon dioxide and the other at about 25 per cent. Hazelhoff (1935) found in experiments with *Periplaneta* and many other insects, that in concentrations of 2 to 3 per cent, carbon dioxide causes opening of the spiracles and at 10 per cent, induces respiratory movement. It would be interesting to know if animals living in logs are so affected. If they are, it would be even more important that they remain in an atmosphere of high humidity, since evaporation of water occurs largely through the spiracles when they are open (Mellanby, 1935).

Toleration of High Temperatures

The results of the experiments show that *Chrysobothris* sp. had the highest thermal death point of any of the larvae investigated and that its death point was not influenced by relative humidity. Compared with the other larvae its loss of water was considerably lower. In any experiment where insects are subjected to a fatal combination of relative humidity and temperature there is a question as to which of these factors actually cause death: i.e., is death due to heat or to desiccation or to a combination of the two? There are considerable data on the limits of desiccation of insects, all of which indicate that considerably more water can be lost by insects without fatal results than was lost by the larvae in this experiment. The meal worm, *Tenebrio molitor*, has been investigated by several authors, who show that more than 50 per cent of its body weight can be lost without loss of vitality (Hall 1922, Buxton 1930, Mellanby 1934). Therefore, it seems most likely that death of *Chrysobothris* sp. was due to the effects of heat alone. These results are similar to those reported by Mellanby (1932) on fleas and meal-worm larvae, in which he shows that the thermal death of these forms is also unaffected by humidity for short periods of time. Graham (1924) reports the thermal death point of *Chrysobothris dentipes* adults as varying from 45 to 52°C., but did not give the method by which he arrived at these figures. The larvae used in the writer's experiments agree with the upper limit he reports, but they did not show such variation.

The resistance of *Chrysobothris* sp. to desiccation is similar to that of species living in dry material, although not as marked as in the case of *Tenebrio molitor*. Since *Chrysobothris* sp. forms its hibernating cell in the relatively thin, dry bark of oak, usually less than one-half inch from the

surface, it is to be expected that it would be subjected at times to low humidities. The relative humidity surrounding insects in such cells in wood is not known, and it would not be safe to draw conclusions as to the humidity of the air around the larva from the dryness of the wood. Fidler (1936) has shown that chafer larvae (Scarabidae) form an earthen cell around themselves in which they are able to maintain a higher humidity than that of the surrounding atmosphere. If *Chrysobothris* sp. can maintain a relative humidity in the atmosphere surrounding it which is greater than that which would naturally be produced from moisture in the wood, it can do so only by a constant evaporation of moisture from its body, since there is no impervious material lining the cells. The moisture in the air around the larva would be absorbed by the wood when the moisture content of the latter became lower than that which it would contain at the relative humidity around the larva. This follows from the fact that wood absorbs a definite amount of water from the atmosphere at different humidities, and reaches a moisture equilibrium with the atmosphere at a particular humidity (Hawley and Wise, 1926).

The ability of *Chrysobothris* sp. to withstand high temperatures and low humidities is significant in view of its habits. It is well known that most species of the Buprestidae are thermophilic forms, mating and laying their eggs in places exposed to the sun. Graham (1925) showed that the larvae of *Chrysobothris dentipes* occurred only on the top side of pine logs in the sun where the subcortical temperatures were highest. The writer's observations, made while collecting from both pine and oak logs, are in accord with Graham's experimental work. *Chrysobothris* sp. lays its eggs in timber exposed to the sun and its young, by virtue of their adaptations to high temperature and low humidity, are able to live in situations that are intolerable to many other insects.

Monochammus titillator, Romaleum atomarium, and *Acanthocinus nodosus* may be considered together since they gave similar results. It is apparent from the results obtained with these species that humidity had an effect on their thermal death point. The larvae of each of these species were able to survive a higher temperature in an atmosphere of low humidity than in a saturated atmosphere or one 90-95 per cent saturated. This phenomenon has been encountered by other workers using different species of insects. Mellanby (1935) reviewed the literature on the subject and based his explanation of the phenomenon on the fact that the body temperature of an insect is lowered in a dry atmosphere by the evaporation of water from its body (Necheles 1924, Mellanby 1932). He points out that only larger insects (above 100 mg.) are able to be cooled enough in this way to affect their thermal death points. The results of the writer's experiments can be explained on the same basis. The fatal temperature in a saturated or nearly saturated atmosphere probably represents more closely the intensity of heat that a larva is able to withstand. At temperatures above this fatal limit a

larva in a dry atmosphere is able to keep its body several degrees cooler than its surroundings for short periods of time by the evaporation of water.

The relation of *Monochammus titillator*, *Romaleum atomarium*, and *Acanthocinus nodosus* to high temperature may be correlated with the conditions in which they live. They are normally found only where the wood is moist and where the humidity of the air around them is probably always near the saturation point. Furthermore they are not found in parts of a log where the subcortical temperature is likely to be as high above the air temperature as it is in the parts inhabited by *Chrysobothris*.

The thermal death point of the larvae of *Dendroides bicolor* is not affected by humidity. This can be explained by the fact that they have a large surface area in relation to their weight, because of their small size, and thus absorb more heat per unit of body weight than do larger forms. In addition, the amount of water that can be evaporated from their bodies is not sufficient to maintain their body temperature below that of their surroundings for a very long time. The larvae of *Dendroides bicolor* are found under the bark of pine and oak logs that have been dead longer than a year, and in which the bark has been loosened from the sapwood by various phloem feeders. They are never found on the top side of logs exposed to the sun, but are only in situations where the temperature under the bark rises but little above the air temperature and where the humidity is near saturation. They are active, and the looseness of the bark makes it possible for them to migrate to a part of the log where conditions are favorable.

NUTRITION OF WOOD BORERS

From the results of the tests for starch in the phloem being eaten and the feces produced by *C. antennatum* and *Chrysobothris* sp., it is concluded that they are able to digest and remove starch from the phloem that they eat. That both species feed for the most part, if not exclusively, on the phloem is shown by the results of the examination of their feces and the frass in the burrows. The significance of this selection of the thin layer of phloem that lies between the cork bark and the xylem, appears to be a difference in the nutritive value of xylem and phloem. At least one of these differences is the greater amount of starch in the phloem. Since the phloem layer becomes quite thin when a log dries out, a larva feeding in it would have to gnaw out a burrow either in the cork bark or in the xylem to accommodate its increase in size as it grew older. This explains the uneaten frass dug from the xylem. Apparently the xylem plays no part in their nutrition.

Since the dry weight of the larvae of *Callidium antennatum* and *Chrysobothris* sp. is correlated with the area of their burrows and the calculated dry weight of phloem that they eat, the two species must have approximately an equal amount of growth on an equal amount of wood. Whether the phloem in the various logs from which larvae were collected had the same nutritive value or not is not known. It seems probable, however, that if they had

differed greatly, a greater difference in the relation between the dry weight of individual larvae and the area of their burrows, and thus in the amount of wood eaten, would have been obtained. It will be observed in Fig. 8 that the relation between the dry weight of a larva and the amount of wood it ate is fairly constant for every individual.

The amount of starch in the phloem of the logs in which larvae of *C. antennatum* and *Chrysobothris* sp. were found is not known and can only be inferred from the analysis of phloem from similar trees cut in November of the following year. These samples had an average starch content of 5 per cent. It is doubtful that from these results it can be safely assumed that the same percentage of starch obtained in logs containing larvae of *C. antennatum* and *Chrysobothris* sp. The reason for this is that no detailed knowledge is available for the seasonal variation of starch in pines in North Carolina or, in fact, at any place in the United States to the writer's knowledge. Pines are classified by Busgen (1931) as "fat trees" because they store large amounts of a fatty material as well as starch. Studies made in Europe by Antevs (quoted by Busgen, 1931) show that there is a conversion of starch to fat; high temperatures, the reverse. Other factors that may affect the amount of starch are the season and the number of years since a seed crop was borne (Busgen, 1931). It is thus clear that, until much more data are obtained, predictions of the amount of starch in pines cannot be made. It is therefore impossible, from the results obtained in the present study, to come to any very definite conclusions as to the amount of starch consumed by *C. antennatum* and *Chrysobothris* sp. with the phloem they ate.

The phloem-feeding cerambycid larvae tested for a cellulase were *Monochammus titillator, Acanthocinus nodosus, Callidium antennatum, Rhagium lineatum, Romaleum atomarium.* None of these larvae showed a cellulase in their gut contents nor did they possess intestinal protozoa or bacteria that could be considered as playing a part in their nutrition. The possibility of the presence of mycetomes, however, has not been excluded, but the work of Mansour and Mansour-Bek (1934a, 1934b) has placed any digestive function of these bodies very much in doubt. Cellulose digestion by the larvae investigated seems, therefore, rather improbable. If utilization of cellulose by the larvae is excluded, the question arises as to what substances in the phloem serve as their source of carbohydrate. Fungi can be excluded because the larvae often begin their burrows in weakened or recently dead trees in which there is little or no fungal growth. It is generally recognized that living phloem is richer in starches, sugars, and proteins than the xylem (Busgen, 1931). The possibility that insect larvae might be able to subsist entirely on the stored starches, sugar, and protein in the phloem is apparent. The author has shown that the living phloem of shortleaf pine contained as much as 5 per cent starch in November and that the larvae of *Callidium antennatum* living on pine phloem remove starch from the wood

they eat. Mansour and Mansour-Bek (1934a) showed that the larvae of a cerambycid could live in wood containing 3.9 per cent starch without attacking the cellulose. Parkins (1936) found that the larvae of species of Lyctus depended on starch in wood for their source of carbohydrates. It is, therefore, probable that the starches and sugars in phloem can furnish the necessary carbohydrates for *Callidium antennatum*. While it has not been shown that the other phloem-feeding larvae investigated digest the starch, it seems likely that they would. It has often been assumed that insects living in wood possessed remarkable digestive powers, because they were believed to be living on cellulose. It has only been in recent years that attention has been called to the fact that many insects may live on materials in wood other than cellulose. In fact, cellulose-digestion in insects has been shown for only a few species (Mansour and Mansour-Bek, 1934b). It is probably significant that there are many insects that attack the phloem of trees as soon as they are dead or even when they are in a weakened condition, in view of the fact that phloem contains more protein, starches and sugars than xylem.

The absence of a cellulase in the larvae of insects feeding in rotten wood (*Passalus cornutus, Pseudolucanus capreolus, Polymoecus brevipes*, and *Scolecocamp liburna*) does not necessarily mean that they are unable to derive nourishment from cellulose. The presence of symbiotic protozoa and bacteria must be taken into consideration. Wiedemann (1930) showed that certain scarabid and lucanid larvae contain bacteria in their gut that digested part of the cellulose in the wood ingested by the larvae. He also found that these beetle larvae digested part of their intestinal bacteria and thus were able to benefit from their presence. Wiedemann did not find cellulase in the larvae he investigated. The scarabid *Polymoecus brevipes* and *Pseudolucanus capreolus* are similar to the larvae investigated by Wiedemann (1930) in that they feed on rotting wood, possess intestinal bacteria in great numbers, lack cellulase, and belong to genera closely related to the genera studied by Wiedemann.

How the other species of rotten-wood feeding larvae investigated obtain available carbohydrates from their food is not known. The results of the writer's experiments show that they do not secrete a cellulase. Whether these species depend on intestinal symbionts or derive carbohydrates from other sources remains to be determined. No symbiotic protozoa were found in the gut of *Alobates pennsylvanica*. The writer has observed that *Alobates pennsylvanica* was always found in wood in which "white-rot" fungi were growing. The possibility is suggested that their nutrition is in some way associated with the type of decay of the wood. Recent work by Boswell (1938) has shown that certain fungi attacking pine, break down cellulose into hexose, and pentose compounds much more rapidly than these compounds are utilized by the fungus. It therefore seems quite possible that certain types of rotting

wood might contain enough digestible carbohydrates, other than cellulose, to supply the needs of an insect feeding on the wood.

The presence of a cellulase in the gut of *Derobrachus brunneus* is of particular interest. The larvae of this species are some of the largest of the cerambycids. They feed in both rotten pine and oaks. In pines they were observed feeding on wood in a very advanced stage of decay, so rotten, in fact, that it could be easily torn to pieces with the hands. In oaks they were observed feeding in the solid heartwood of a rotten log that had been dead about five years. In other oak logs, they were feeding in sapwood attacked by a "white-rot" fungi. While it can not be definitely stated the cellulase found is secreted by these larvae, it is probable that this is the case, since no intestinal protozoa or bacteria were found in their gut that could account for the presence of cellulase.

GENERAL DISCUSSION OF FOOD RELATIONS

Several ecological groups of animals characteristic of logs may be separated on the basis of their food habits:

(a) Wood-boring insects, chiefly the larvae of Coleoptera and Hymenoptera. Certain forms are characteristic of sound wood, while others are found feeding only on rotten wood.

(b) Associated with these xylophagous species are parasitic Hymenoptera and Diptera, and certain predacious beetles that are stenophagous and are thus similar to parasites.

(c) Another group consists of predacious species that are general feeders, such as *Alaus oculatus*.

(d) A fauna distinct from the xylophagous insects includes those feeding on fungi, or relying on their presence in rotting wood. These are chiefly beetles, dipterans, mites, and collembolans. These also have parasites and predators, that are regularly associated with them.

(e) A secondary fauna associated with logs are predatory species that are general feeders such as certain carabids, centipedes, spiders, and ants that visit logs in the course of their hunts for food in the forest floor.

(f) Other species incidentally associated with logs are species that find suitable nesting or hiding places in rotten wood such as bees and wasps. Other species hibernate under bark and in the wood that are not otherwise found there, such as hornets, wasps, and lizards.

This classification is essentially that given by Brues (1927).

Sound wood is eaten by a large number of insects that apparently are able to derive all their food from the stored products in wood. Other insects are able to live on wood as a result of the activities of symbiotic protozoa or bacteria in their guts, while still other species, such as the cerambycid *Derobrachus brunneus* have developed the ability to digest cellulose (Mansour and Mansour-Bek, 1935).

Brues (1927) points out that xylophagous Coleoptera, Hymenoptera, and Lepidoptera constitute part of what may be considered a primitive fauna that has long been characteristic of wood. Xylophagous Hymenoptera and Lepidoptera, in particular, are some of the more primitive members of these orders, and Brues considers that these orders probably arose from ancient lignivorous forms.

Certain parasitic groups living today, such as the Oryssidae, show close affinities to phytophagous Hymenoptera and are thought to have been derived from primitive xylophagous Hymenoptera. If such is the case, it is significant that today the Oryssidae are ecto-parasites of buprestid larvae living in wood.

In many cases it is not possible to be certain whether insects eating rotting wood derive their food substance from fungi in the wood or from the wood itself. Certain species feeding on rotting wood such as *Dendroides canadiensis* and *Synchroa punctata* undoubtedly are dependent on fungi (Payne, 1931). The gut contents of other species show that they probably feed exclusively on fungus spores and hyphae. Certain insects found under bark, such as species of Staphylinidae, Tenebrionidae, Cisidae, and Melandryidae have also been reported as feeding on the fruiting bodies of various wood-rotting fungi, particularly of the genus Polyporus (Weiss, 1920).

One of the striking things about the fauna of logs is the important part played by predacious species in controlling the number of xylophagous and mycetophagous forms. This has been commented on by Fiske (1907) in discussing the enemies of wood-boring Coleoptera. He pointed out that wood-boring insects, as compared to external feeders, had a relatively small variety of parasites. Certain predacious species are stenophagus, as Fiske (1907) and Brues (1927) pointed out. The clerid *Thanasimus dubius* feeds almost entirely on bark beetles, both in its larval and adult stage. The carabids, *Tachyta nana* (Gyll) and *Tachymenis flavicauda* Say, probably get most of their food by preying on mites and collembolans. Further, certain Histeridae, such as *Cylixtix cylindrica* are probably predacious on fly larvae. In contrast to such predators are those such as an ostomid, *Temnochila viverscens*, and the elaterids, *Alaus myops* and *A. oculata* which feed on a variety of xylophagous larvae.

SUMMARY

1. During the period from September, 1936 to February, 1938 about 280 logs, 155 pines and 125 oaks, were examined in the Duke Forest, Durham, North Carolina.

2. There is a succession of animals in pine and oak logs from the time they are cut until they disintegrate.

3. Insects feeding in the phloem of pine and oak logs during the first year after they are cut prepare the way for the entrance of fungi and a subcortical fauna including mycetophagous and predacious species. A sub-

cortical fauna in oaks may enter spaces formed between the bark and wood by the shrinkage of sapwood. The environmental changes in logs leading to a succession of wood-feeding animals appear to be largely those caused by fungi.

4. Subcortical temperatures under the loose bark of pine logs exposed to sunlight in summer rose as much as 11°C. above air temperature when the latter was 33°C.

5. Temperatures under the bark and at various depths in sapwood of logs fluctuate with air temperatures in all seasons of the year with a lag depending in part on the depth in the log at which temperatures are taken. Animals under bark probably receive little protection from low temperatures in winter in the Duke Forest. It is suggested that for many animals logs are more important as hibernacula because of their moisture content rather than the protection they afford from low temperatures, though logs do moderate extreme and rapid changes.

6. Temperatures in rotting logs were not perceptibly affected by heat that might have been produced by fungi or other organisms, or by possible auto-oxidative processes within the wood.

7. Samples of air taken from under bark and from rotting wood of logs contained as much as 5.53 per cent (volume) carbon dioxide, and oxygen concentration as low as 15.53 per cent (volume).

8. The highest temperature of two hours duration tolerable to larvae of *Chrysobothris* sp. (probably *femorata* Oliv.) taken from oak logs, was 52°C. regardless of the relative humidity in which they were exposed. Toleration of *Chrysobothris* sp. to such high temperature may be correlated with the fact that it lives on the top side of oak logs exposed to the sun.

9. The highest temperature of two hours duration tolerable to *Romaleum atomarium*, *Monochammus titillator*, and *Acanthocinus nodosus* was 49°, 50°, and 46° respectively, when exposed in air with a relative humidity of approximately 10-15 per cent. With relative humidity of 100 per cent they could only tolerate temperatures of 44°, 44°, and 43°C., respectively. The explanation offered for this phenomenon is that the cooling effect of evaporation of water from a larva in dry air undoubtedly lowers its body temperature below that of its surroundings.

10. The highest temperature of two hours duration tolerable to larvae of *Dendroides bicolor* was 41°C. in humidities of both 10-15 and 90-95 per cent. It is considered that their small size prevents them from being able to lose enough water by evaporation to maintain a lower body temperature than their surroundings.

11. Loss of water from larvae tested for toleration to high temperatures was proportional to the temperatures at which they were exposed, when relative humidity was 10-15 per cent.

12. Of the larvae tested, those of *Chrysobothris* sp. were most resistant to

desiccation, and those of *Dendroides bicolor* least resistant. The percentage of body weight lost by evaporation from larvae of *Romaleum atomarium*, *Monochammus titillator*, and *Acanthocinus nodosus* was intermediate between that of *Chrysobothris* sp. and *Dendroides bicolor*. The difference in the larvae investigated with respect to their resistance to desiccation may be correlated with the conditions of moisture in the logs in which they live.

13. The average dry weight of the phloem covering one square centimeter of area on shortleaf pines was found to be 0.0555 ± 0.0021 grams.

14. The amount of starch in three samples of living phloem collected from shortleaf pine in November was 5.02 per cent of the dry weight of the sample.

15. The larvae of *Callidium antennatum* and *Chrysobothris* sp. feed on the phloem of pine poles containing as little as 26 per cent water. They eat little, if any of the sapwood which they dig out in making their burrows. In poles which contained larvae the sapwood contained no starch, but the phloem contained enough starch to be turned blue-black by iodine.

16. Larvae of *Callidium antennatum* and *Chrysobothris* sp. remove starch from the phloem they eat.

17. The areas of the burrows that had been formed by ten larvae of *Callidium antennatum* and four larvae of *Chrysobothris* sp. up until they had formed pupal chambers, were determined. The areas of the burrows measured were proportional to the dry weights of the larvae that had made them. From the average dry weight of the phloem covering one square centimeter of surface on shortleaf pine, the amount of phloem that had probably been consumed by larvae of both species was calculated. The dry weights of phloem probably consumed were proportional to the dry weights of the larvae. The average amount of phloem (dry weight) that had been eaten by a larva (dry weight); for *Chrysobothris* sp. it was 77.1 ± 3.1 grams.

18. The gut contents of five larvae feeding on rotting wood and five larvae feeding on phloem were tested for the presence of a cellulase with negative results. Cellulase was found in the gut contents of the larvae of *Derobrachus brunneus*, which feeds in solid and soft rotting wood.

19. Larvae of beetles feeding on phloem of logs less than one year old are probably able to derive all their essential food from products stored in the cells of the phloem without digesting cellulose.

20. The gut contents of 22 species of insects of doubtful food habits were examined. Some were found to be predacious, others fed on fungus hyphae and spores, rotting wood, or both.

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APPENDIX

In the following lists the animals collected from pine and oak logs are given. The numerals immediately following the scientific name refer to the ages of logs from which the species was collected; next follows the location on or in the log where it was usually found; next follow the stages in life history that feed in the log; then the relative abundance of the species, whether common, occasional, or rare; and finally the food eaten. In the latter, the asterisk following the food means that the observation was made by the author. The food of certain species has been inferred from a knowledge of related species. An asterisk following a reference means that it refers to a related species.

I. Animals Collected from Pine Logs

Collembola

Entomobrya sp.; 1, 2, 3, 4; under bark in rotten wood; all; decayed wood, fungi.

Pseudachorutes sp.; 1, 2; under bark; all; occasional; decayed wood, fungi.

Isotoma sensibilis Tlb.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Entomobrya ligata Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Tomocera flavescens Tlb. var. *Americanus Schott;* 1, 2; under bark; all; common; decayed wood, fungi.

Entomobrya corticola Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Isoptera

Reticulitermes flavipes Koll.; 2, 3; rotting wood; all; common; sapwood*.

Orthoptera

Parcoblatta sp.; 1, 2, 3, 4; under bark, under logs; all; common; omnivorous, Blatchley (1920).

Heteroptera

Undetermined; 1; under bark; all; common; predacious on scolytids*.

Homoptera

Epiptera sp.; 1; under bark; all; rare; fungi.*

Coleoptera

Galerita bicolor Drury; 1, 2, 3; on log under bark; adult; occasional predacious, Forbes (1883).

Clivina sp.; 2, 3, 4; on log under bark; adult; occasional; phytophagous, Blatchley (1910)*.

Tachymenis flavicauda (Say); 1, 2, 3, 4; under bark; adult larva; common; Collembola mites*.

Atheta sp.; 2, 3; under bark; adult larva; occasional; fungi?

Erchomus ventriculus Say; 1, 2; under bark; adult larva; common; fungi?

Nudobius cephalus (Say); 1, 2; under bark; adult larva; common; predacious?

Alcocharinae gen. sp.; 1, 2, 3, 4; under bark in rotten wood; adult larva; common; fungi?

Saprinus sp.; 1, 2; under bark; adult larva; common; predacious*.

Platysoma parallelum Say; 1, 2; under bark; adult larva; common; predacious*.

Platysoma parallelum Say; 1, 2; under bark; adult larva; common; predacious*.

Plegaderus sp.; 1, 2, 3; under bark in rotten wood; adult larva; occasional; fungi*.

Cylistix cylindrica (Payk.); 1, 2; under bark; adult larva; common; predacious probably fly larvae*.

Platysoma lecontei Mars.; 1, 2, 3, 4; under bark in rotting wood; adult larva; common; predacious*.

Plateros floralis Melsh.; 1; under bark; larva; rare; predacious*.

Thanasimus dubius Fab.; 1; under bark on log; adult larva; common; bark beetles*. Fiske (1907).

Cymatodera sp.; 2; under bark; larva; occasional; predacious? Weiss (1922)*.

Copidita thoracica Fab.; 3; rotting wood; larva; common; rotting wood*.

Boros unicolor Say; 1, 2; under bark; larva; occasional; fungi, rotting wood*.

Dendroides bicolor Newn.; 1, 2; under bark; larva; common; fungi*, rotting wood.

Alaus myops; 1, 2, 3, 4; under bark in rotting wood; larva; common; predacious*, general beetles.

Ischiodontus sp.; 1, 2; under bark; larva; common; rotting wood*.

Orthostethus infuscatus Germ.; 3, 4; rotting wood; larva; common; rotten wood*.

Melanotus sp.; 1, 2, 3, 4; under bark in rotting wood; larva; common; rotten wood*.

Elater verticinus Beauv.; 1, 2, 3, 4; under bark in rotting wood; common; rotten wood*.

Megapenthes limbalis (Hbst.); 2, 3; under bark; larva; occasional; rotten wood*.

Drapites sp.; 1, 2, 3; under bark; larva; common; rotten wood?

Buprestis lineata Fabr.; 1, 2; phloem, sapwood; larva; common; phloem, sapwood*.

Buprestis sp.; 1, 2, 3; phloem, sapwood; larva; common; phloem, sapwood*.

Chalcophora sp.; 1; phloem; larva; common; phloem*.

Chrysobothris sp.; 1; phloem; larva; common; phloem*.

Temnochila virescens (Fab.); 1; under bark; larva adult; common; predacious* general feeders.

Tenebroides collaris Sturm.; 1; under bark; adult larva; common; predacious*.

Rhizophagus cylindricus (Lec.); 1; under bark; adult larva; occasional; predacious on scolytids?

Brontes dubius Fab.; 1, 2, 3; under bark; adult larva; common; fungi*.

Mycetophagus pini Zieg.; 1, 2; under bark; adult larva; occasional; fungi, Weiss (1922)*.

Colopterus semitectus Say; 1; under bark; adult larva?; common; sap, Blatchley (1910)*.

Stelidota geminata Say; 1; under bark; adult larva?; common; sap, Blatchley (1910)*.

Pycnomerus sulcicollis Lec.; 2; under bark; larva; common; predacious?

Colydiidae sp.; 2; under bark; larva; predacious?

Penthelispa haematodes Fab.; 2; under bark; adult larva; common; predacious?
Penthelispa reflexa Say; 2; under bark; adult larva; common; predacious?
Synchita sp.; 2, 3; rotten wood; larva; common; rotting wood*.
Uloma punctulata Lec.; 3, 4; rotten wood; adult larva; common; rotten wood*.
Xylopinus rufipes (Say); 2, 3, 4; rotten wood; larva; common; rotten wood*.
Scotobates calcaratus (Fab.); 3, 4; rotten wood; larva; common; rotten wood*.
Alobates barbata (Knoch); 2; under bark; only adults found; occasional; probably hibernating.
Bolitotherus cornutus (Panz); 1; under bark; adult larva?; occasional; fungi*.
Hypophloeus parallelus Melsh.; 1; under bark; adult larva?; occasional; predacious? Schwartz (1889)*.
Platydema flavipes Fab.; 1, 2, 3; under bark; adult larva; common; fungi*.
Hypulus concolor (Lec.); 2; rotting wood; larva; occasional; rotten wood*.
Stephanopachys rugosus Oliv.; 1, 2; sapwood; larva; common; sapwood*.
Passalus cornutus Fab.; 3, 4; rotting wood; adult larva rare; rotten wood*.
Pseudolucanus capreolus (L.); 3, 4; rotting wood; larva; rare; rotten wood*.
Derobrachus brunneus (Forst.); 4; rotting wood; larva; occasional; rotten wood*.
Asemum moestum Hald.; 1; phloem, sapwood; larva; common; phloem, rotting sapwood*.
Rhagium lineatum Oliv.; 1; phloem; larva; common; phloem*.
Xylotrechus sagittatus (Germ.); 1; phloem; larva; rare; phloem*.
Callidium antennatum Newn.; 1; phloem; larva; common; phloem*.
Acanthocinus obsoletus (Oliv.); 1; phloem; larva; common; phloem*.
Aconthocinus nodosus (Fab.); 1; phloem; larva; common; phloem*.
Eupogonius tomentosus Hald.; 1; phloem; larva; rare; phloem*.
Monochammus titillator (Fab.); 1; phloem; larva; common; phloem*.
Leptura sp.; 2; 3; rotten wood; larva; present; rotten wood*.
Rhyncolus sp.; 1, 2, 3; under bark; adult larva; rare; probably fungi.
Cossonus corticola Say; 1, 2, 3; under bark; adult larva?; common; fungi*.
Pissodes memorensis Germ.; 1; phloem; larva; common; phloem*.
Pachylobius picivorus Germ.; 1; phloem; larva; rare; phloem*.
Hylobius pales Hbst.; 1; phloem; larva; common; phloem*.
Platypus flavicornis Fabr.; 1; sapwood; adult larva; common; fungi in its burrow.
Ips grandicollis Eichh.; 1; phloem; adult larva; occasional; phloem*.
Ips calligraphus Germ.; 1; phloem; adult larva; common; phloem*.
Xyleborus fitchi Hopk.; 1; sapwood; adult larva; occasional; fungi*.
Orthotomicus caelatus (Eichh.); 1; phloem; adult larva; common; phloem*.
Pityophthorus annectens Lec.; 1; phloem; adult larva; occasional; phloem*.
Pityophthorus pullus Simm.; 1; phloem; adult larva; occasional; phloem*.
Dendroctonus valens Lec.; 1; phloem; adult larva; common; phloem*.
Dendroctonus tenebrans (Oliv.); 1; phloem; adult larva; common; phloem*.

Diptera

Forcipomyia sp.; 2; under bark; larva; rare; unknown.
Chironomidae (undetermined); 3, 4; rotten wood; larva; common; fungi? Curran (1934)*.
Sciara coprophila Lint.; 1, 2; under bark; larva; occasional; reared from dead cerambycid.
Cecidomyidae (undetermined); 3, 4; rotten wood; larva; common; fungi? Harris (1923)*.
Xylopaagus fasciatus Walker; 1; under bark; larva; occasional; predacious on *Rhagium lineatum**.

Dolicopodidae (undetermined); 2, 3, 4; rotten wood; larva; occasional; fungi? Curran (1934)*.

Phoridae (undetermined); 1, 2; under bark; larva; common; predacious; Curran (1934)*.

Lonchaea sp.; 1, 2; under bark; larva; common; bacteria or fungi, Curran (1934)*.

Theresia monohammi (Ins.); 1; under bark; larva; common; parasite of *Monochammus titillator*.

Sarcophaga repax Walker; 1; under bark; larva; common; parasite of *Monochammus*.

Hymenoptera

Sirex migricornia Fab.; 1; sapwood; larva; occasional; sapwood.

Oryssus sp.; 1; under bark; larva; common; parasite of *Chrysobothris* sp.

Atanycolus sp.; 1; under bark; larva; rare; parasite host unknown.

Coeloides pissodis Ashm.; 1; under bark; larva; common; parasite of *Pissodes nemorensis*.

Coeloides (striatus Prov.); 1; under bark; larva; occasional; parasite host unknown.

Coeloides sp.; 1; under bark; larva; occasional; parasite host unknown.

Pristaulacus resutovorus (Westw.); 1; under bark; larva; occasional; parasite unknown.

Trypioxlyon clavatum; 2, 3; nests in cerambycid burrows; larva; common; probably spiders or insects.

Halictus (Chloralictus) sp.; 4; nests in rotten wood; larva; common; poiren.

Camponotus herculeanus (*pennsylvanicus* DeG.); 1, 2, 3; nests in sapwood or bark; adults and larvae; common; predacious and scavengers, Wheeler (1913).

Crematogaster lineota Say; under bark; adults; common; scavengers, Wheeler (1913).

Leptinothorax curvispinosus Mayr.; 1, 2, 3, 4; under bark; adults; common; scavengers, Wheeler (1913).

Ponera coarctata (*pennsylvanica* Emery); 1, 2, 3, 4; under bark; adults; occasional; scavengers, Wheeler (1913).

Lasius umbratus mixtus Nyl.; 1, 2; under bark; adults; occasional; scavengers, Wheeler (1913).

Annelida

Lumbricidae (undetermined); 3, 4; under bark in rotten wood; all stages; common; rotten wood*.

Mollusca

Polygyra thyriodus Say; 4; under log in rotten wood; adults; occasional; rotten wood fungi?

Euconulus chersinus Say; 2, 3; under bark; adults; common; rotten wood fungi?

Zonitoides arboreus Say; 2, 3, 4; under bark; adults; common; rotten wood fungi?

Philomycus carolinensis (Bosc.); 3, 4; in rotten wood; adults; occasional; rotten wood fungi?

Myriapoda

Cambala annulata Say; 3, 4; under logs in rotten wood; adults; common; rotten wood*.

Fontaria coriacea Koch; 2, 3, 4; under logs in rotten wood; adults; common; rotten wood*.

Polydesmus serratus (Say); 4; under logs in rotten wood; adults; common; rotten wood*.

Geophilus varians McNeil; 1, 2, 3, 4; under bark; adults; common; predacious.

Linotaenia bidens (Woods); 1, 2, 3, 4; under bark; adults; common; predacious.

Cryptops hyalina Say; 1, 2, 3; under bark; adults; common; predacious.

Bothropolys multidentatus Newport; 1, 2, 3; under bark; adults; occasional; predacious.

Chelanops oblongus; 1, 2; under bark; all stages; common; predacious* small larvae probably mites.
Chelanops virginnae; 1, 2; under bark; all stages; common; predacious.
Chelifer cancroides; 1, 2; under bark; all stages; common; predacious.

Acarina

Uropoda sp. (several species); 1, 2, 3, 4; under bark; all; common; unknown.
Trachyuropodidae (undetermined); 1; under bark; all; unknown.
Parasitus sp.; 1, 2; under bark; all; common; certain species are probably predacious.
Dendrolaelaps sp.; 1, 2; under bark; all; common; certain species are probably predacious.
Pergamasus sp.; 1, 2; under bark; all; common; certain species are probably predacious.
Several undetermined species; 1, 2, 3, 4; under bark; all; common; certain species are probably predacious.
Tyroglyphidae (undetermined); 2, 3; under bark; all; common; certain species are probably predacious.
Allothrombium pulvinus Ewing; 2; under bark; all; occasional; predacious?
Orabatidae (several undetermined sps.); 2, 3; under bark; all; occasional.

Vertebrata

Plethodon glutinousus (Green); 4; under logs in rotten wood; adult; occasional; probably various insects.

II. Animals Collected from Oak Logs

Collembola

Entomobrya ligate Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.
Lepidocyrtus cyaneus Tlb.; 1, 2, 3; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.
Isotoma sensibilis Tlb.; 1, 2, 3, 4; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.
Pseudistoma sensibilis Tlb.; 1, 2, 3; under bark in rotten wood; occasional; fungi and rotten wood? Essig (1926).
Pseudachorutes sp.; 2, 3; under bark; all; occasional; fungi*.
Neosmithurus clauatus (Banks); 2, 3, 4; under bark; all; rare; fungi?

Thysanura

Machilis variabilis Say; 2, 3, 4; under bark; adult; common.

Isoptera

Reticulitermes flavipes Koll.; 2, 3, 4; sapwood; all; common; rotting wood*.

Zoraptera

Zorotypus hubbardi Caudell; 2, 3; under bark; all; rare; fungi?

Orthoptera

Parcoblatta sp.; 1, 2, 3, 4; under bark; all; common; omnivorous? Blatchley (1920)*.

Heteroptera

Mezira granulata Say; 2, 3, 4; under bark; all; common; predacious? Essig (1926).
Systelloderus biceps; 2, 3; under bark; all; common; predacious?

Homoptera

Epiptera sp.; 2, 3; under bark; all; occasional; fungi*.

Coleoptera

Tachyta nana (Gyll); 1, 2, 3, 4; under bark in rotten wood; all; common; mites and collembola*.

Harpalus pennsilvanicus (De Geer); 2; under bark; adult; rare; predacious, Forbes 1883)*.

Agonum (?punctiforme Say); 2; under bark; adult larvae?; rare; predacious?

Bolitobius cinctus Grav.; 4; rotten wood; all; common; predacious? Mank (1923)*.

Hesperus baltimorensis (Grav.); 4; rotten wood; all; common; predacious*.

Gastrolobium lecontei (Horn); 1, 2, 3; under bark; all; common; predacious*.

Conosoma crassus (Grav.); 1, 2, 3, 4; under bark in rotten wood; all; common; fungi*.

Thoracophorus costalis Er.; 1, 2, 3; under bark; all; occasional; scavenger? fungi.

Staphylinus violacens Grav.; 3, 4; under bark in rotten wood; all; common; predacious*.

Tachinus fembriatus Grav.; 4; rotten wood; all; common; predacious? Mank (1923).

Coproporus ventriculus Say; 3, 4; under bark; all; common; scavenger fungi?

Trachysectus confluentus Say; 3, 4; under bark; all; common; fungi*.

Philonthus sp.; 1, 2, 3, 4; under bark; larvae adult? common; predacious Mank (1923)*.

Batrisodes? sp.; 4; rotten wood; larva adult? occasional; mites? Blatchley (1910).

Actium sp.; 4; rotten wood; larva adult? occasional; mites Blatchley (1910).

Acritus exiguus (Er.); 1, 2; under bark; all; common; fungi*.

Bacanius punctiformis Lec.; 2, 3; under bark; all; common; fungi?

Epierus regularis Beauv.; 2, 3, 4; under bark; all; occasional; fungi?

Epierus sp.; 2, 3, 4; under bark; all; fungi?

Platysoma carolinum (Payk.); 2, 3, 4; under bark in rotten wood; all; common; predacious*.

Platysoma lecontei Mars; 2, 3, 4; under bark in rotten wood; all; common; predacious*.

Charicssa pilosa Forst. sub-sp. *Marginata* Say.; 1, 2, 3; under bark; larva adult? common; predacious Felt (1906).

Mordellistena sp.; 2, 3; rotten wood; larva; rare; rotten wood*.

Glipodes sericans Welsh; 3; rotten wood; larva; occasional; rotten wood*.

Dendroides bicolor Dru.; 2, 3, 4; under bark; larva; common; rotten wood* fungi.

Elater nigricollis Hbst.; 2, 3, 4; under bark in rotten wood; larva; common; rotten wood*.

Orthostethus infuscatus (Germ.); 3, 4; rotten wood; larva; common; rotten wood*.

Deltometopus amoenicornis (Say); 4; rotten wood; larva; occasional; rotten wood*.

Alaus oculatus Linn.; 1, 2, 3, 4; under bark in rotten wood; larva; common; predacious*.

Melanopus sp.; 1, 2, 3; under bark in rotten wood; larva; common; rotten wood*.

Adelocera sp.; 2, 3; under bark in rotten wood; larva; common; predacious*.

Eleterinae (undetermined); 2, 3, 4; under bark in rotten wood; larva; common; rotten wood*.

Chrysobothris femorata (Oliv.); 1; phloem; larva; common; phloem*.

Agrilus sp.; 1, 2; phloem; larva; common; phloem*.

Dicerca sp.; 2; phloem; larva; occasional; phloem*.

Ptilodactyla sp.; 4; rotten wood; larva adult; rare.

Ptilodactyla serricollis Say; 2; rotten wood; larva adult; rare.

Rhysodes americanus Lap.; 4; rotten wood; larva adult; occasional; rotten wood.

Tenebroides sp.; 3; under bark; larva adult; rare; predacious.

Silvanus embellis Lec.; 1, 2; under bark; larva adult; common; fungi*.

Silvanus planatus Germ.; 1, 2; under bark; larva adult; common; fungi*.

Brontes dubius Fab.; 1, 2, 3, 4; under bark; larva; common; fungi*.

Lachmophloeus sp.; 1, 2; under bark; adult; common; predacious Schwartz (1889).
Megalodacne fasciata (Fab.); 1, 4; under bark; larva adult; occasional; fungi*.
Triplax thoracica Say?; 4; rotting wood; larva adult?; occasional; fungi*.
Mycetyphagidae (undetermined); 4; rotting wood; larva adult?; common; fungi?
Coxelus guttulatus Lec.; 2; under bark; larva adult; occasional; predacious?
Penthelispa reflexa Say; 2, 3, 4; under bark; larva adult; common; predacious.
Synchita fuliginosa Melsh.; 2; rotting bark; larva adult?; common; rotting bark.
Solydium lineola Say; 3; burrows of *Platypus* sp.; larva adult; occasional predacious on scolytids Felt (1905).
Hymenorus sp.; 4; rotten wood; larva adult?; common; rotten wood.
Hoplocephala bicornis Oliv.; 2, 3; under bark; larva adult; common; fungi*.
Platydema subcostatum Lap.; 2, 3, 4; under bark; larva adult; common; fungi*.
Platydema ruficorne Sturm.; 2, 3, 4; under bark; larva adult; common; fungi*.
Platydema ruficolle Cast. and Brll.; 2, 3, 4; under bark; larva adult; common; fungi*.
Uloma imberbis Lec.; 3, 4; rotten wood; larva adult; common; rotten wood*.
Dioedus punctatus Lec.; 3, 4; rotten wood; larva adult?; common; rotten wood*.
Scotobates calcaratus (Fab.); 3, 4; rotten wood; larva; common; rotten wood*.
Merinus laevis Oliv.; 2; rotten wood; larva; rare; rotten wood*.
Xylopinus saperdoides (Oliv.); 3, 4; rotten wood; larva; common; rotten wood*.
Alobates pennsylvanicus (DeG.); 2, 3, 4; rotten wood; larva; common; rotten wood*.
Meracantha contracta (Beauv.); 4; rotten wood; larva; common; rotten wood*.
Strongylium crenatum Makl.; 4; rotten wood; larva; common; occasional; rotten wood*.
Synchroa punctata Newm.; 2, 3, 4; under bark; larva; common; rotten wood* fungi.
Phlocotrya vaudouere Muls.; 2, 3; rotten wood; larva; common; rotten wood*.
Cis sp.; 2; under bark; larva adult?; common; fungi; Blatchley (1910).
Pseudolucanus capreole (L.); 3, 4; rotten wood; larva; common; rotten wood*.
Platycerus quercus Web.; 4; rotten wood; larva adult? occasional; rotten wood*.
Ceruchus piceus (Web.); 4; rotten wood; larva adult? occasional; rotten wood*.
Dorcus (*brevis* Say?); 4; rotten wood; larva adult? occasional; rotten wood*.
Polymoecus brevipes Lec.; 4; rotten wood; larva; common; rotten wood*.
Cloetus globosus (Say); 4; rotten wood; larva adult? rare; rotten wood*.
Trichiotinus bidens Fab.; 4; rotten wood; larva; occasional; rotten wood*.
Phileurus valgus L.; 4; rotten wood; larva; rare; rotten wood*.
Passalus cornutus Fab.; 2, 3, 4; rotten wood; larva adult; common; rotten wood*.
Derobrachus brunneus (Forst.); 4; rotten wood; larva; common; rotten wood.
Leptura proxima Say; 4; rotten wood; larva; common; rotten wood.
Xylotrechus colonus (Fab.); 1; phloem; larva; common; phloem.
Romaleum atomarium (Drury); 1, 2, 3; phloem, rotten wood; larva; common; phloem.
Neoclytus scutellaris Oliv.; 1; phloem; larva; rare; phloem.
Graphisurus fasciatus DeG.; 1, 2; phloem; larva; common; phloem.
Eupsalis minuta Drury; 3, 4; rotten wood; larva adult? occasional; solid and rotten wood Felt (1905).
Euparius marmoreus Oliv.; 3; under bark; larva adult? occasional; fungi Blatchley (1916).
Platypus quadridentatus Oliv.; 3; in sapwood; larva adult; common; fungi* (Ambrosia).
Orthotomicus coelatus Eichh.; 1; under bark; larva adult; common; phloem*.

Lepidoptera

Scolecocampa liburna Geyer; 3, 4; rotten wood; larva; common; rotten wood*.

Diptera

Megaselia sp.; 1, 2; under bark; larva; common; predacious? Curran (1934).
Lonchaea sp.; 1, 2; under bark; larva; common.

Tipula trivittata Say; 4; rotten wood; larva; rare.
Teucholabis sp.; 4; rotten wood; larva; rare.
Palpomyia sp. (undetermined species); 3, 4; rotten wood; larva; common.
Mycetophilidae (undetermined); 2, 3, 4; rotten wood; larva; common; fungi Baumberger (1918).
Cecidomyidae (undetermined); 3, 4; rotten wood; larva; common; micro-organisms? Baumberger (1918)*.
Dolicopodidae (undetermined); 2, 3, 4; rotten wood; larva; common; micro-organisms? Baumberger (1918)*.
Oscinella sp.; 4; rotten wood; larva.
Tachinidae (undetermined); 1; larva; common; parasite on *Romaleum atomarium*.

Hymenoptera

Tremex columba L.; 1, 2; sapwood; larva; occasional; sound wood*.
Atanycolus simplex (Cress.); 1; under bark; larva parasite; common; parasite of *Chrysobothris fermorata**.
Atanycolus sp.; 1; under bark; larva parasite; host unknown.
Atanycolimorpha n. sp.; 2; under bark; larvae parasite; in *Romaleum atomarium**.
Sparhius floridanus Ashm.; 1; under bark; larvae parasite; common; in *Chrysobothris fermorata**.
Doryctes n. sp.; 2; under log; larva parasite; from scarabid larva.
Augochlora pura Say; 4; rotten wood (nesting); larva adult; common; pollen*.
Vespula maculata (L.); under bark; occasional; not feeding, hibernating.
Camponotus herculeanus pennsylvanica DeG.; 1, 2, 3, 4; under bark in rotten wood; larva adult; common, scavengers? Wheeler (1913).
Crematogaster lineolata Say; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).
Leptothorax curvispinosus Mayr.; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).
Ponera coarota pennsylvanica Emery; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).
Proceratium croceum; 1, 2, 3, 4; under bark in rotten wood; larva adult; occasional; scavengers? Wheeler (1913).
Formica exsectoides Forel; 3; under bark in rotten wood; adults; occasional; scavengers? Wheeler (1913).
Pheidole sp.; 4; rotten wood; all adults; rare; scavengers, Wheeler (1913).

Annelida

Lumbricidae (undetermined); 3, 4; under bark in rotten wood; all; common; rotten wood*.

Mollusca

Strobilops aena Pilsbry; 3, 4; under bark; all; common; rotten wood fungi?
Polygyra fallax Say; 4; rotten wood; all; rare; rotten wood fungi?
Polygyra tridentata Say; 4; rotten wood; all; occasional; rotten wood fungi?
Polygyra thyroidus Say; 4; rotten wood; all; rare; rotten wood fungi?
Zonitoides arboreus Say; 2, 3, 4; under bark; all; common; rotten wood fungi?
Euconulus chersinus Say; 2, 3, 4; under bark; all; common; rotten wood fungi?
Retinella indentata Say; 2, 3, 4; under bark; all; common; rotten wood fungi?
Philomycus carolinensis (Bosc.); 3; 4; under bark in rotten wood; all; common; rotten wood fungi?

Myriapoda

Cambala annulata (Say); 3, 4; under bark; all; occasional; rotten wood?
Fontaria coriacea Koch; 4; under bark under log; all; rotten wood*.
Polydesmus serratus Say; 4; under bark under log; all; rotten wood*.
Spirostrephon lactarium (Say); 3, 4; under bark under log; all; rotten wood*.
Linotaenia bidens (Woods); 1, 2, 3; under bark; all; common; predacious.
Geophilus varians (McNeil); 1, 2, 3; under bark; all; common; predacious.
Scolopendra viridis Say; 2, 3, 4; under bark in rotten wood; all; common; predacious.
Cryptops hyalina Say; 2, 3, 4; under bark in rotten wood; all; common; predacious.
Otocryptops sexspinosus (Say); 2, 3, 4; under bark in rotten wood; all; rare; predacious.
Bothropolys multidentatus Newport; 2, 3, 4; under bark in rotten wood; all; occasional; predacious.

Chelonethida

Chthonius spinosus; 1, 2; under bark; all; occasional; predacious.
Chthonius longipalpus; 1, 2; under bark; all; occasional; predacious.
Chelanops sp.; 3; under bark; all; occasional; predacious.
Chelanops dentatus; 4; under bark; all; rare; predacious.

Acarina

Podothrombium sp.; 4; under bark; all; occasional; predacious?
Allothrombium pulvinus Ewing; 4; rotten wood; all; common; predacious?
Zetes sp.; 3, 4; under bark; all; occasional; fungi?
Schelorabates sp.; 4; under bark; all; common; fungi?
(Undetermined specimens); 3, 4; under bark; all.
Uropoda sp. several species; 1, 2, 3; under bark; all; common; saprophytic?
(Undetermined species); 1, 2, 3; under bark; all; saprophytic?
Discopoma sp.; 1, 2, 3; under bark; all; saprophytic?
(Undetermined species); 1, 2, 3, 4; under bark; all; saprophytic?
Pergamasus sp.; 1, 2, 3, 4; under bark in rotten wood; all; common; predacious?
Scilus sp.; 2, 3; under bark in rotten wood; all; predacious?
Megisthanus sp. 1, 2, 3, 4; under bark in rotten wood; all; common; predacious?
Dendrolaelops sp.; 1, 2, 3; under bark in rotten wood; all; predacious?
(Undetermined species); 1, 2, 3, 4; under bark in rotten wood; all.
Tyroglyphidae (undetermined species); 2; under bark; all; common.

Vertebrata

Plethodon glutinosus (Green); 4; rotten wood under logs; adults; occasional; predacious?